# A Theoretical And Empirical Investigation Of The τ-Coupling Theory

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Doctor of Philosophy

The University of Edinburgh

1998

# Declaration

I hereby declare that this thesis was composed by myself and that the work within it is my own.

Signed Madeleine Grealy

Date 20th October 1998

# Acknowledgements

I would like to thank my supervisors Professors David Lee and Ian Donaldson for their support and guidance during this period of study. In particular I would like to thank David Lee for discussions on the theoretical ideas and his enthusiasm for my work. Thanks must also go to Cathy Craig for her invaluable advice and encouragement, and to all my subjects for their patience and co-operation. Finally, I would like to thank Simon and the rest of my family for their continued help and support.

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# Abstract

Understanding how movements are controlled is a difficult and elusive problem. Many different theories have been proposed but each has its faults and limitations, and so, as yet, no unifying and comprehensive theory of action exists. This thesis is concerned with assessing a new theoretical perspective to see if it can improve our understanding. This theory, the τ-coupling theory, takes its philosophical basis from the ecological psychology movement. It is a psychological theory about perception-action couplings, and is formally stated in mathematical terms. It proposes how the closures of gaps are co-ordinated.

In this thesis the plausibility and generality of the τ-coupling theory, and in particular the constant acceleration intrinsic τ-guide hypothesis, are assessed from three different perspectives. The first of these is in terms of oculomotor control. A comparison is made between the systems models and τ-coupling theory in the control of gaze shifting. The results suggest that the present formulation of systems models do not fully account for the behaviour observed, and a new model for gaze control, based on τ-coupling, is presented.

The biological plausibility of this theory is further investigated in a study of the actions of AM, a patient with cerebellar damage. The data indicate that AM was able to τ-couple his movements onto a constant acceleration intrinsic τ-guide in certain situations which required his actions to be controlled proprioceptively. However, in more complex situations, especially those involving vision, his τ-coupling ability was compromised. It is concluded that the cerebellum is involved in the use of visual information in τ-coupling.

The extent to which the constant acceleration intrinsic τ-guide hypothesis can account for the control of a range of movements, and in particular reaching movements, was also assessed. The conclusion drawn is that, in its present form, this hypothesis can account for behaviour only if several assumptions are met. The first of these is that the gap has to be perceived prior to movement onset. The second is that if τ-coupling is going to account for a significant proportion of an action then that action must be discrete, that is start and end at rest. Finally, the actor needs to be able to accurately define the duration of the movement.

It is concluded that while the τ-coupling theory has advanced our understanding of how perception and actions might be integrated and controlled, the intrinsic τ-guide hypothesis does not describe a unifying fundamental law because it lacks generalization to non-discrete movements. Finally, while it seems that τ information might exist in some form in the central nervous system, the biological mechanism remains to be determined.

# Chapter 1: τ Theory

## 1.1 Introduction

From observing a normal human adult in their daily activities it would appear that the control of a purposeful movement is a simple and seemingly effortless task, yet, for the scientist attempting to explain such control it quickly becomes apparent that this simplicity masks a high degree of complexity. Producing a definitive theory of movement control is proving to be a difficult task. It is also one which has been tackled by many researchers from various disciplines, and since these researchers often differ in their philosophical beliefs and the research paradigms they adopt, it is not surprising that this area is full of controversies and conflicting ideas. In particular, different theoretical positions have been shaped according to beliefs on the nature of perception and on the role that sensory information plays in the control of action. However, while there are many differences between the numerous models, they tend to have one thing in common; they have all, to some extent, been influenced by the work of the Russian scientist Nikolai Bernstein.

In 1967 Bernstein pointed out that theoretical modelling involves the use of a construct, often mathematical, to describe a highly complex system. He believed that such models were not descriptions of systems but ways of thinking about them that could be used to generate ideas. Today's modellers, however, do not all accept Bernstein's views on the utility of their work. They want their models to provide accurate explanations of how the brain operates, not mere descriptions that provoke new lines of thought. They intend to search for fundamental laws. This thesis is

concerned with one such model known as τ-coupling. This model, which is encompassed in the general τ theory, was proposed by Lee and colleagues (Lee et al., 1995, Lee et al., 1998a, Lee et al., 1998b) as a possible explanation for how purposeful movements are controlled.

τ theory is an ecological theory of prospective movement control, and its development and ethos were greatly influenced by the philosophy of J.J. Gibson. His stance (Gibson, 1966) was in opposition to that of the empiricists who believed that sensations need to be elaborated upon to form adequate mental representations of the outside world. He rejected the notion of dualism and insisted that the distinction between sensory and motor aspects of behaviour is artificial. Instead, he proposed that the changes brought about by motor behaviour should be thought of as an integral part of perceiving, and that the meaning that the environment has for an organism shapes its behaviour. He believed that perception is an activity and frequently stressed the importance of movement in perception.

Gibson also proposed the concept of invariants and this idea greatly influenced the development of the τ theory. Invariants are the higher order properties of patterns of stimulation that remain constant in different circumstances, such as, for example, when an observer moves in a particular way relative to any environment. The τ theory aims to show how certain temporal properties of actions are invariant; that is it defines perceptuo-motor characteristics which remain stable across different situations.

1.2 τ Theory

τ is a temporal measure of a gap, and in his early work Lee (1976) demonstrated that the changes in optic flow that occur when moving through an environment correspond to the spatiotemporal properties of the action. This relationship can be defined mathematically and Lee was able to show that the first-order time remaining before the mover makes contact with an object is specified by the inverse of the rate of dilation of the optical image of the object (τ). This corresponds to the gap between the mover and object divided by the velocity of approach (1).

$$\frac{1}{\text{rate of dilation of optical image}} = \frac{\text{distance between observer and object}}{\text{velocity of gap closure}} \qquad (1)$$

The left hand side of equation (1) is the negative of τ of the width of the optical image and the right hand side is the τ of the physical gap.

Lee (1993) went on to demonstrate that one salient source of information that can be used in the controlled closure of gaps is $\dot{\tau}$, the rate of change of τ. Many studies have reported that the regulation of braking is controlled so that $\dot{\tau}$ is kept constant (Lee et al., 1991, 1992a,1992b,1993, 1995, Yilmaz and Warren, 1995), and the constant $\dot{\tau}$ strategy has been recognised in different species and across different actions.

Recently, the validity of the τ theory has been questioned (Tresilian, 1990, 1993, Wann, 1996). These criticisms will be addressed more fully in Chapter 6, but at this point it will suffice to say that, for the most part, these criticisms are based on the popular misconceptions concerning the τ theory, and in particular that it is solely

concerned with gap information specified by the optical expansion of images. This is not so. The general theory states that $\tau$ can be perceived in any sensory modality, and information from different sensory $\tau$s has been found to be used in the controlled closure of gaps (Lee et al. 1995, 1998a, 1998b, Craig and Lee, 1997).

While the criticisms of the constant $\dot{\tau}$ strategy have mainly resulted from a misunderstanding of the general $\tau$ theory, there are two issues which question the extent to which the $\dot{\tau}$ idea can be considered as a global concept in a theory of motor control. Firstly, $\dot{\tau}$ only accounts for braking movements, so it cannot explain movements with acceleration as well as deceleration phases. Secondly, the constant $\dot{\tau}$ strategy is only concerned with the closure of single gaps, it does not account for how two or more gaps can be closed synchronously, as is frequently the case in skilled actions. In response to these problems Lee and colleagues (Lee et al., 1995, 1998a, 1998b, Craig and Lee, 1997) proposed the concept of $\tau$-coupling.

## 1.3 $\tau$-Coupling

$\tau$-coupling is a theory about the co-ordination of gap closures. The term 'gap' is used to describe the difference between a current state and a desired goal, and can be thought of in terms of the distance which needs to be covered, the angle that needs to be turned, or the force that needs to be exerted to accomplish a particular task. However, before a gap can be closed it must first be perceived, and the theory proposes that properties within sensory flow fields give rise to 'temporal guides' that can be used to initiate and direct the closure of a gap. Once started, a movement creates perceptual changes in sensory flow fields; that is, the temporal

closure of a physical gap ($\tau_{Movement}$) results in a corresponding change in the $\tau$ of the gap measure in the sensory flow field ($\tau_{Sensory}$). However, a sensory $\tau$ is not necessarily determined by a single flow field such as optic flow. In fact cases where this could occur are limited. Rather it is more likely to be an amalgamation of information from various flow fields. The notion of perception-action coupling, which was central to the early ideas on $\tau$ (Lee, 1976), has been expanded in the $\tau$-coupling theory to account for how the closure of two or more gaps could be co-ordinated.

The basic idea of $\tau$-coupling is that the synchronous closure of two gaps can be achieved by keeping the $\tau$s of the gaps in a constant ratio. Such a strategy ensures that gaps of different magnitudes, that are being closed at different rates, will reach zero simultaneously. This can be described mathematically as

$$\tau_X = k\tau_Y \qquad (2)$$

where $\tau_X$ and $\tau_Y$ correspond to the first-order time-to-closure of gaps x and y, and k is a constant which describes the kinematics of the closure. If $0<k<0.5$ the closure of gap x will be gentle since the velocity of closure will be low just prior to contact, but if $0.5<k<1$ the closure of gap x will be more abrupt because the velocity of closure will be greater just prior to contact.

Prior to movement onset, the expropriospecific information about the gaps an actor wishes to close can be either dynamic or static, and this distinction helps determine whether the coupling will be extrinsic or intrinsic. In dynamic situations where an object is moving towards a goal, the temporal closure of this gap can

provide a guide onto which the actor can couple their movement τ. This kind of action has been called an 'extrinsic τ-coupling' (Lee et al., 1998b).

A demonstration of an extrinsic τ-coupling was provided by Lee et al. (1998a). In this task the subject was presented with a target which moved diagonally across a computer screen (from bottom left to top centre), and their task was to move a pointer (from bottom centre to top centre on the screen) so that they 'caught' the target at a designated point. That is, subjects had to time their movement so that the gap between the target and the goal, and the gap between the pointer and the goal reached zero at the same time. The results indicated that subjects achieved this by coupling the τs of the gap between the hand and the catching place, and the gap between the hand and the moving object. By keeping these two τs in a constant ratio the hand reached the catching place at the same time as the moving object. It was concluded that the τ-coupling was achieved using an extrinsic τ-guide (τ of the hand to object). Thus, an extrinsic τ-guide can be defined as the perceptual variable (specified by expropriospecific information relating to the changing nature of one physical gap), that can be used to 'create' a movement τ that will close another physical gap.

While extrinsic τ-coupling adequately explains the behaviour observed by Lee et al. (1998a) there are many other instances in which there is no extrinsic τ-guide that can be used to prospectively control an action. These are self determined movements in which the goal and the timing of the action are defined intrinsically (by the mover) and not extrinsically. The theory states that in such cases movements are controlled using an intrinsically generated τ-guide onto which the τ of the effector

can be coupled. An intrinsic τ-guide (τg(t)) is an internalised representation of the changing first order time to closure of a gap at each time t. The choice of an appropriate intrinsic τ-guide is based on the kind of action that the environment affords and predictions based on similar experiences. The coupling between the intrinsic τ-guide and the τ of an effector requires on-line prospective control, and Lee et al. (1998b) conceive of the coupling which uses an intrinsic τ-guide as being the same as the coupling that involves an extrinsic guide, except for the fact that the extrinsic guide is sensed perceptually, while the intrinsic guide is generated internally.

At present the existence of an intrinsic τ-guide is still a matter of speculation, however, if it were to exist then it must account for the observable kinematic patterns of movements, such as the ubiquitous bell-shaped velocity profile. In order to try and establish the validity of this idea Lee et al. (1998b) have devised a mathematical model for an intrinsic τ-guide, based on a premise of evolutionary parsimony. They propose that an intrinsic τ-guide would utilise a simple adjustable low order motion parameter and take the form of either constant velocity, constant acceleration or constant deceleration. As shown in Appendix I, the constant acceleration form generates, via coupling, a bell shaped velocity profile. Both the constant velocity and constant deceleration τ-guides could not account for this velocity profile.

The constant accelerating intrinsic τ-guide can be conceptualised as starting from rest and accelerating towards its goal at a constant rate. It has a single

adjustable parameter namely its duration (T), and as the derivations in Appendix I show it can be described mathematically as

$$\tau_g(t)=0.5((t-T^2)/t) \qquad (3)$$

where T equals the total duration of the movement, and t equals the time from when the guide starts. When a movement $\tau$ is coupled onto a constant accelerating intrinsic $\tau$-guide the velocity profile of the movement is dependent on the value of the coupling constant k. As Figure 1.1 indicates as the value of k increases the period of acceleration increases and the time at which peak velocity occurs moves closer towards the end of the movement.

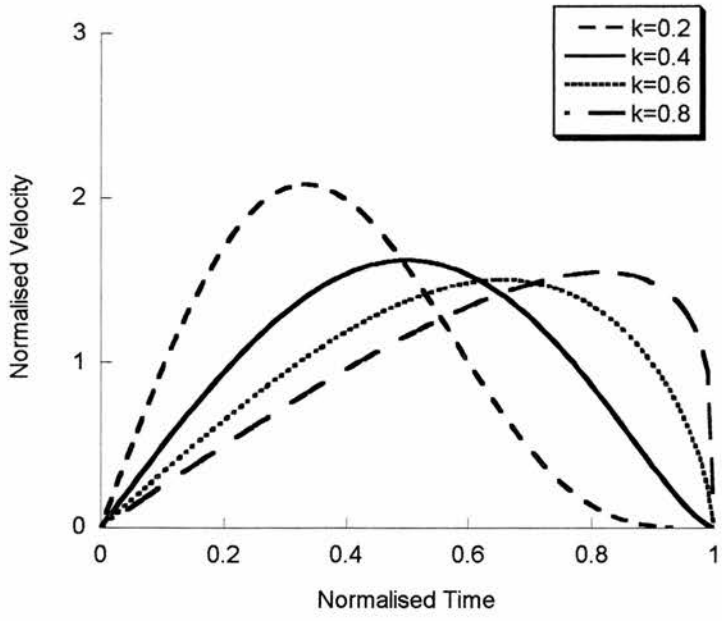


Figure 1.1 Velocity profiles of a hypothetical movement that would result if the movement $\tau$ was coupled to an intrinsic $\tau$-guide ($\tau_{movement}=k\tau_{guide}$) with different values of k.

Overall, the intrinsic τ-guide theory has an appealing simplicity; only two parameters are needed to account for the control of a movement; the duration (T) and the coupling constant (k). It also proposes that instead of having a series of control parameters which relate to distance, angle or force, along with their first and second derivatives, that there is a much simpler solution; namely, the first order time to closure (τ).

## 1.4 Evidence for the τ-Coupling Theory

The intrinsic τ-coupling theory was tested using a paradigm of proprioceptive control, moving the hand to the mouth (Lee et al., 1998b). In this experiment six healthy right-handed adults were asked to pick up a grape or a small sweet between the thumb and index finger and raise it to their mouth. They each completed sixteen trials, eight with their eyes shut and eight with their eyes open, in a random order. On each trial they tilted their head back to an unusual position, so as to assume a different angle of tilt on each trial. The movement of finger to mouth was recorded using a Selspot$^{TM}$ camera positioned with its optical axis perpendicular to the plane of movement of the finger. The camera recorded the (x,y) coordinates of three infra-red light emitting diodes attached to the finger, nose and chin respectively. A typical trial is shown in Figure 1.2.

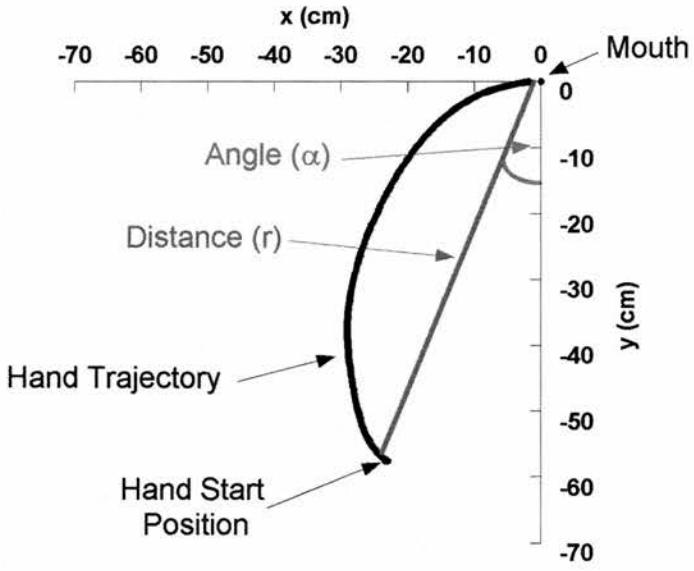


Figure 1.2 The trajectory of one trial where the finger was moved towards the mouth (point (0,0) ). The angle ($\alpha$) and distance (r) were calculated for each point along the trajectory.

From observing the data it appeared that during the movement the subject was simultaneously controlling the distance between the finger and the mouth (r, Figure 1.2) and the angle of approach ($\alpha$, Figure 1.2). For each trial, the values of $\tau_{\alpha-\alpha_{final}}$ and $\tau_{r-r_{final}}$ relative to a mouth frame of reference were calculated every 3.2msecs and the degree of $\tau$-coupling was assessed between the angular gap, the distance gap, and an intrinsic constant acceleration $\tau$-guide since this was a self paced movement,

From equation (2) it can be seen that if two $\tau$s are coupled then plotting one $\tau$ against the other will result in a straight line which has a slope equal to k. The strength of different couplings can be assessed by estimating the degree to which the $\tau$-$\tau$ plot is straight. A recursive linear regression procedure was used to determine

when various couplings started and the percentage of the total movement time that each of the couplings accounted for was calculated.

(a) Linear Regressions for $\tau$-guide /\/\ $\tau_r$ (b) Linear Regressions for $\tau_r$ /\/\ $\tau_\alpha$

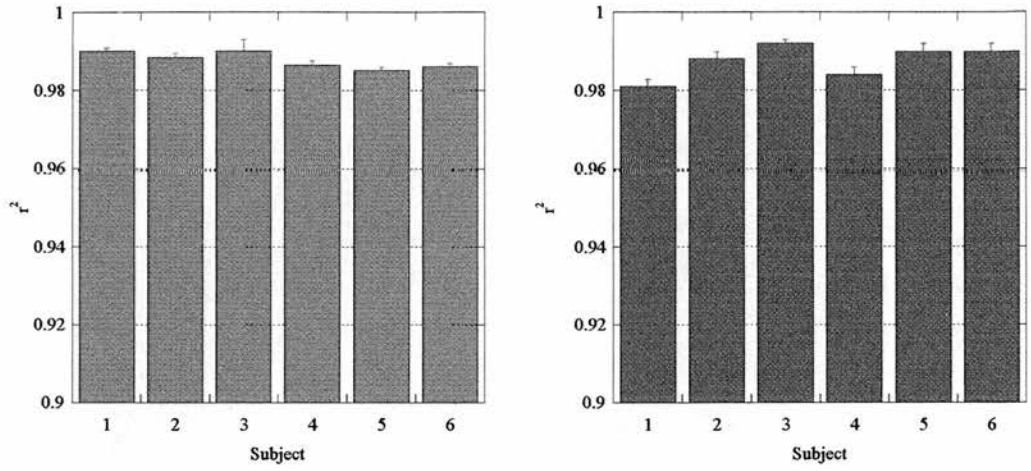


Figure 1.3 Mean and standard deviations of $r^2$ of the linear regressions for the plots of (a) $\tau$-guide coupled to $\tau_r$ and (b) $\tau_r$ coupled to $\tau_\alpha$ in trials where the subjects eyes were closed. The symbol /\/\ is used to indicate coupling.

The results indicated that the movement of the hand to the mouth was controlled by two $\tau$-couplings: $\tau_r$ was coupled to $\tau$-guide, and $\tau_\alpha$ was coupled to $\tau_r$. Figure 1.3 shows that linear regressions for the plots of $\tau_r$ against $\tau$-guide and $\tau_\alpha$ and $\tau_r$ were very close to one, and Figure 1.4 shows that these couplings accounted for at least eighty percent of the movement.

(a) Coupling duration for $\tau$-guide /\ $\tau_r$ (b) Coupling duration for $\tau_r$ /\ $\tau_\alpha$

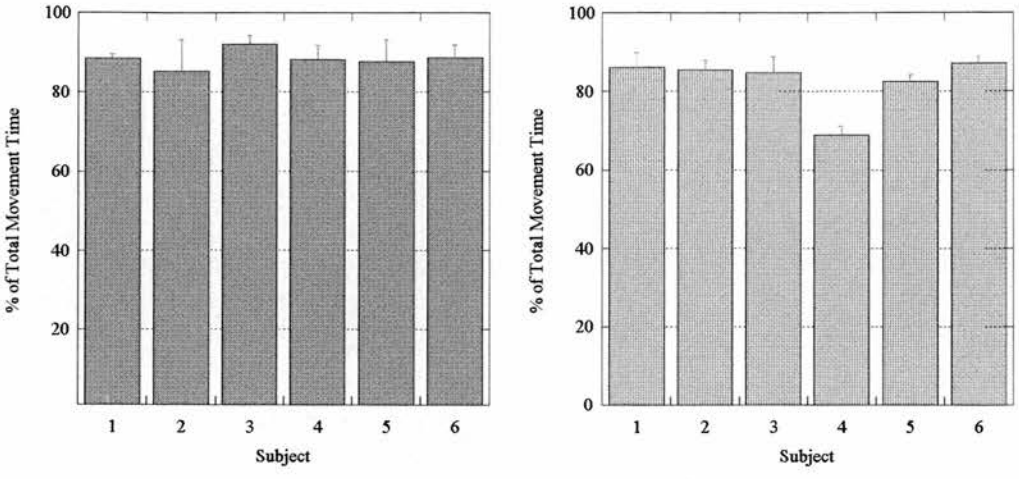


Figure 1.4 Mean and standard deviations of the percentage of the total movement time that $\tau$-guide was coupled to $\tau_r$ (a) and $\tau_r$ was coupled to $\tau_\alpha$ (b) for trials where the subjects eyes were closed.

Further evidence for $\tau$-coupling has come from the work of Craig (1997) and Craig and Lee (1997) on infant sucking behaviour. They showed that healthy infants were able to demonstrate a $\tau$-coupling strategy during the increasing suction phase of a suck. This strategy involved keeping the ratio of an intrinsic $\tau$-guide to $\tau_{pressure}$ constant. Pre-term infants on the other hand were less capable of doing this.

Together these research findings show that co-ordinated actions can be described in terms of $\tau$-coupling, and they indicate that $\tau$-coupling may be both a powerful and comprehensive theory of movement control. However, for this theory to be generally accepted as an adequate explanation for the control of purposeful actions it will be necessary to show that it has generality and that it fits with known

biological facts. The aim of this thesis is to examine the extent to which the τ-coupling theory satisfies these two requirements.

# Chapter 2 : Theories of Motor Control

## 2.1 Introduction

The τ-coupling theory is radically different from other theories of movement control and, as a consequence, it challenges the beliefs currently held by many researchers. In particular, the use of an intrinsic τ-guide is controversial since it appears to reflect the idea of a motor programme. The question of how such a guide may be neurally represented is also an issue; is it a metaphor or is it a physical entity? The purpose of this chapter is to examine these issues in the light of previous research and to establish ways in which the generality and biological plausibility of the τ-coupling theory might be assessed.

The chapter will start by examining the concept of the intrinsic τ-guide and its relationship to previous theories that have used the idea of an engram or a motor programme. It will then go on to discuss the relationships between the τ theory and two major groups of theories found in the literature on motor control; theories on single joint arm movements and theories of eye movements.

## 2.2 Engrams, Motor Programmes and Intrinsic τ-Guides

Any particular intrinsic τ-guide can be defined as a time varying quantity, $\tau_g$ (t), that corresponds in value to the τ of a closing gap. It is an internally generated temporal representation which is analogous to some quantity which starts from rest and accelerates at a constant rate towards its goal level. These properties ensure that, via τ-coupling, an appropriate movement τ for the closure of a physical gap will

be generated. The duration (T) of the τ-guide is determined prior to the movement onset, and is the only adjustable parameter that is needed to establish the guide. It is hypothesized that an intrinsic τ-guide is used during self paced movements and situations where there is no expropriospecific information that could act as an external guide.

The idea that movements are controlled using an internally generated plan is not new, but this idea of an intrinsic τ-guide is being proposed at a time when the concept of a motor programme is being challenged. However, as many have pointed out, the definition of a motor programme is far from fixed, and, as an analysis of how this term has been used will show, the kind of motor programme that Lee et al. (1998b) are proposing is somewhat different from the commonly accepted version. This does not necessarily mean however, that it provides answers to all of the documented theoretical problems.

In writing about the neural representation of movement Bernstein (1935) recognised the need to establish the 'correct formulation of categories which are really represented in brain centres'. He went on to elaborate upon what he believed constituted a category and how such categories are neurally encoded using two ideas; the principle of equal simplicity and the engram. Subsequently, these two ideas have profoundly influenced the theoretical developments on the nature and use of motor programmes. However, it seems that while many modern theorists have adopted the physiological ideas proposed by Bernstein they have failed to incorporate his underlying belief that it is actions, not just movements, that are controlled.

Bernstein used the principle of equal simplicity to try and overthrow the old localisation concept and show that movements could be classified in terms of their invariant characteristics. A classic example of this principle is the demonstration that when writing on different scales, the phasing and timing of writing movements remains relatively constant even though the task of writing in large letters requires the involvement of different muscles to those used when writing in small letters. Thus, 'the transition from one element of the set of possible tasks to another' has a negligible effect on performance. In support of his ideas Bernstein quoted Lashley (1929), who had demonstrated a lack of relationship between the destruction of different areas of the cortex and the degree to which 'reconditioned reflexes' could be re-established. Bernstein reasoned that instead of having a system whereby specific muscles are controlled by specific brain centres, the central nervous system has diverse innervation patterns that produce specific movements, and diverse neural centres that have variable degrees of involvement in the co-ordination of specific actions. In doing so he pre-empted, or perhaps inspired, those theorists working some fifty or so years later who developed the idea of parallel distributed processing (for example, McClelland and Rumelhart, 1985).

Bernstein (1935) described the neural representation of categories of movements in terms of an engram. He wrote:

"..... there exist in the central nervous system exact formulae of movement or their engrams, and these formulae or engrams contain in some form of brain trace the whole process of the movement in its entire course in time. "

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His conception of an engram was not as a specific movement pattern but, as Reed (1984) pointed out, as a motor gestalt. They were 'images of the movement' and he saw the process of generating movements as one in which

"It is as if an order sent by the higher centre is coded before its transmission to the periphery so that it is totally unrecognisable and is there again automatically deciphered."

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Thus, Bernstein believed that within the brain the dispersed representations of an action are independent of any particular form of movement. In contrast to this the notion that the brain stores specific motor commands that detail complex peripheral movements has created the foundation for a dominant view of motor control; that of the motor programme. This view contends that the central nervous system creates, stores and selects motor programmes that it executes in a hierarchical and serial manner. The idea of a homunculus which oversees the functioning of a generalised motor programme was popularised by Schimdt's Schema theory (1975), and the analogy drawn between the central nervous system and the computer was a prevalent feature of this information processing approach that dominated the literature from the late 1960s to the end of the 1980s. The motor programme approach has not been without its critics though, and among the main causes for concern has been the problem of establishing a neural basis for a programme and solving the problems of inverse kinematics and dynamics. These problems refer to how such a system could cope with the complexity of computation

that would be necessary to accurately define the changes in joint angles and muscle forces for a particular action. Since these could be both numerous and complex for even a simple action, the notion of a motor programme that specifies these parameters is an unlikely candidate for motor control.

Perhaps the most significant challenge to the concept of a motor programme has come from neurobiologists. They have argued against the view that the central nervous system is an algorithmic processor, and suggested that the motor programme's only use is to demonstrate a lack of understanding about the neural basis of motor control. In defence of theories such as Schimdt's, it must be said that they were formulated at a time when relatively little was known about the structure and functional organisation of the motor system, and it was hoped that future research would reveal the appropriate neural mechanisms. The observations made by Marsden (1982) on patients with basal ganglia disease appeared to support the notion that lower structures play a role in the selection or execution of motor programmes. Likewise Rizzolatti's (1983) suggestion that higher cortical structures like the supplementary motor area are involved in motor programming was suggestive that the motor system functions in a similar fashion to that of a Turing machine. However, this has not turned out to be the case.

Alexander and Crutcher (1990) showed that within a single motor area separate neuronal populations exist that represent different 'levels' of processing. Their finding that multiple layers of processing were proceeding concurrently within an area, combined with the realisation that the cortical and basal ganglionic motor circuitry was massively parallel (Alexander et al., 1994), led them to conclude that the conceptualisation of a motor programme as something that is similar to a

computer programme, is biologically implausible. This does not mean that specific areas of the brain do not have a functional specificity though, but it does imply that motor circuits do not require simple one to one links between neurons at successive anatomical levels.

The alternative that has emerged in response to such criticisms is connectionism. As Alexander et al. (1994) noted:

"The essence of most connectionist models is that they are layered self-organising networks of highly interconnected processing units with properties that are in some ways analogous to biological neurons. In connectionist networks information is not stored in discrete locations but in the overall pattern of variable-strength connections among neurons."

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If systems are self-organising this reduces the need for a controller, and solves a problem that has plagued the motor programme approach. This idea has been influential in the formation of models that use the physics of non-linear limit-cycle oscillator systems to describe the dynamical and emergent properties of behaviour (e.g. Kelso, 1997). These models suggest that when a system is perturbed a new pattern of order is created by a means of self organisation. That is, the system acquires a new spatial, temporal or functional structure without the aid of a command programme. Changes in behaviour simply emerge as the system is attracted to a different state making the concept of a motor programme obsolete. While this might seem appealing there are two main weaknesses to this dynamical

systems approach when it is applied to the problem of motor control; first, in order to model a transition from one state to another it is necessary to define the initial system state. If the system under observation is, for example, an infant learning to reach, then it is difficult to see how the initial state of child's neural, muscular and skeletal subsystems can be adequately described in terms of a dynamic equation, and how the interaction between these subsystems can be modelled. Second, these models are only appropriate for continuous rhythmical tasks such as walking or running, they do not account for how discrete actions are controlled. In particular they neglect the role of expropriospecific information in the control of an ongoing action.

Conceptually the idea of a constant acceleration intrinsic τ-guide appears to be much closer to that of a motor programme than a dynamical system. It retains the notion of a controller and a comparator, but due to the nature of the guide their 'jobs' are greatly reduced. In the case of the intrinsic τ-guide all the controller has to do is choose the duration for the movement and a value for the τ-coupling constant, which defines the movement kinematics. This is because all τ-guides are assumed to have a standard form, that is they start from rest and accelerate at a constant rate. With an extrinsic guide the situation is even simpler since the movement τ is directly coupled onto a physical event. The τ theory does not require the central nervous system to make complex computations, a problem that has previously hampered many of the feedforward approaches. Likewise, the comparator simply has to match τs, rather than transform various sensory signals into comparable frames of reference, so its 'workload' is also reduced.

The concept of τ-coupling using an intrinsic τ-guide appears to resolve some of the problems associated with motor programmes, however, in doing so it appears to lose some of the ecological ideas of perception-action coupling that were apparent in the earlier work on τ (Lee, 1976). This is because τ-coupling with an intrinsic τ-guide means that the control of the movement is directed by an internal temporal representation rather than the external motion of an object. This is different to the nature of the prospective control seen in extrinsic τ-coupling where perceptual information is directly available from exteroceptive and exproprioceptive sources. However, Lee et al. (1998b) propose that an intrinsic τ-guide is treated as a perceived τ in the process of τ-coupling. That is, that the prospective control lies in the coupling of the intrinsic and movement τs.

So far the evidence for the τ-coupling theory suggests that intrinsic τ-guides are used when extrinsic τ-guides are not available. Most previous theories of motor control have only considered situations that would require an intrinsic τ-guide because they have used paradigms based on reaching movements made to stationary targets, or just simple single joint movements. While these paradigms have led to many influential models, the general theories that have arisen from them are somewhat restricted in the types of movements they can account for. The next section gives an overview of what many consider to be the dominant theory of motor control to date, the 'equilibrium point hypothesis', and discusses the similarities and differences between this and the τ-coupling theory.

## 2.3 The Equilibrium Point Hypothesis

The equilibrium point hypothesis was originally proposed by Feldman (1966), but since then it has undergone revision (Feldman, 1986) and was reformulated by Bizzi and his colleagues (Polit and Bizzi, 1978, 1979, Bizzi et al., 1982, 1984). The various versions of lambda ($\lambda$) and alpha models that make up this general view are based upon the mechanical spring-like properties of muscles and in particular the length-tension relationships of agonist and antagonist muscles acting around a single joint. They draw upon the findings of Rack and Westbury (1969) who described the effect changing muscle length had on the force that the muscle generated. Holding the muscle at different lengths they stimulated it tetanically via the muscle nerve and measured the force exerted on the tendon using a force transducer. They found that as the length of the muscle increased the force exerted rose to a peak before declining slightly as the muscle reached the extent of its natural length range. This length-tension relationship is often referred to as an invariant characteristic and can be accounted for by the findings of Gordon et al. (1966), who demonstrated that, as the overlap between the actin and myosin filaments in a single sarcomere increases, more cross bridges can form which results in an increase in force. However, when actin filaments begin to 'overlap' cross bridge formation is disrupted and the force declines.

Rack and Westbury (1969) went on to show that the isometric tension that develops in a muscle is not solely dependent upon muscle length but is also related to the level of stimulation. They plotted muscle tension (kg) against muscle length (cm) for a range of frequencies of stimulation and noted that increasing the frequency tended to displace the length-tension curve to the left, and consequently varied the

range of muscle lengths at which tension rapidly increased.

Feldman and Orlovsky (1972) went on to describe how, under fixed levels of stimulation, increasing muscle length beyond a certain point led to a dramatic increase in stiffness, due to the autogenic recruitment of a motoneurons. Increasing the 'descending command' (level of stimulation) caused a parallel shift in the length-tension curve, and the muscle length at which the autogenic recruitment of $\alpha$ motoneurons starts was termed the threshold for the tonic stretch reflex ($\lambda$). The tonic stretch reflex is regulated by the gamma efference input to the muscle spindles. Muscle spindles are fusiform structures that lie in parallel to the muscle fibres and have sensory and motor functions. When a muscle is stretched the spindles are also stretched and this creates changes in the firing patterns of Ia and II afferents arising from them. These afferent signals from the spindles relate to the length and change in length of the muscle. This information is transmitted to the spinal cord where the afferent axons synapse with $\alpha$ motoneurons that innervate the muscle being stretched.

Feldman (1966) proposed that the movement of the forearm could be brought about by simply selecting length-tension curves for the muscles acting on the upper limb so that the torques in the agonist and antagonist muscle would be equal and opposite when the hand reached the desired position. Thus, a shift in $\lambda$ (the threshold muscle length at which motoneurons are recruited) was all that was needed to move the limb to the desired position. In this original version of the $\lambda$ model, $\lambda$ was seen as a centrally supplied variable which defined the position of the length-tension function, the shape of which was dependent upon the invariant

characteristics. In a more recent version (Feldman, 1986) however, λ has been described as a measure of the threshold of motoneuron membrane depolarisation and is acknowledged as being both centrally and peripherally defined

The idea of a motor programme has relied heavily on the use of systems models commonly found in engineering, and in particular the notion of a closed feedback loop. In contrast, the original equilibrium point hypothesis implied two things that are contrary to this approach. Firstly, it assumed that a knowledge of the effector's initial state was not needed, and secondly it claimed that movements occur as a consequence of the biomechanical properties of the system, and not as a result of on-line prospective control. The alpha model proposed by Bizzi and colleagues (Polit and Bizzi, 1978, 1979, Bizzi et al., 1982, 1984) based upon single joint movements made by deafferented monkeys supported the equilibrium point hypothesis, but the evidence for multijoint movements has not been so convincing. Rothwell et al. (1982) demonstrated that without vision deafferented patients made grossly inaccurate movements, whilst vision of the hand prior to a movement has been found to greatly improve accuracy (Ghez et al., 1990, 1995). Furthermore, Lacquaniti et al. (1982) demonstrated that modifications to the inertial properties of the arm did not alter the spatiotemporal characteristics of a movement trajectory, a finding that was contrary to the predictions made by the equilibrium point hypothesis

It also became evident that the trajectory of the movement needed to be accounted for as well as the end point and in order to account for this, and overcome some of the previous difficulties, the concept of a virtual trajectory was proposed (Bizzi et al., 1982, 1994, Hogan, 1984, Feldman and Levine, 1995). This idea was

that since the neural input to a muscle has the effect of selecting different length-tension curves, the central nervous system could specify a whole series of equilibrium points that form a virtual trajectory. The virtual trajectory is seen as a time series of equilibrium points which can be planned without complex computations. The virtual positions that they specify can be thought of as attractors, and the difference between the actual and virtual positions generates a spring-like force that 'pulls' the limb. Changes in movement kinematics are brought about by changing and updating the chosen length-tension curves. For instance, if the limb is required to move more quickly than usual during the acceleration phase of a movement, then the first endpoint to be chosen would be beyond the target. This would ensure that during the first part of the movement the arm would move rapidly. The endpoint could then be adjusted to the target position whilst the movement progressed.

The validity of this idea has recently been questioned using perturbation studies. Coello et al. (1991, 1996) rotated subjects in an armchair and looked at how the subsequent centrifugal and Coriolis forces affected the accuracy and kinematics of fast pointing movements. They found that, initially, the perturbing forces increased the amplitude of the movement and deviated it in a direction opposite to the motion of the chair. Subsequently, the subject learnt to compensate for the perturbation, a process that was reversed when the chair was stopped. Similar results have been found by Lackner and Dizio (1992, 1994) who argued that had the subjects been using a virtual trajectory the initial deviations should not have occurred since the virtual trajectory should have 'pulled' the hand back on course.

Further criticisms of the equilibrium point hypothesis have come from Kawato and colleagues (Katayama and Kawato, 1993, Gomi and Kawato, 1996) who have demonstrated that actual trajectories significantly differed from computationally predicted virtual trajectories, and that the use of a virtual trajectory for fast movements would require a level of stiffness that is biologically implausible.

While these studies create problems for the equilibrium point hypothesis they can more easily be accounted for by the τ-coupling theory. During the perturbations caused by the rotating chair, Coello et al. (1996) noted that the duration of the movements remained stable throughout. Thus, it can be proposed that in compensating for the perturbation the subject would have used the same constant accelerating intrinsic τ-guide, but altered the τ-coupling constant (k). Unlike the equilibrium point hypothesis, which has difficulty in explaining these results, the τ-coupling theory can account for the subject's behaviour in this situation. However, the extent to which τ-coupling could account for perturbations that occur during slow movements still has to be established. Since the duration of an intrinsic τ-guide is pre-set prior to movement onset and cannot be modified during the execution of the movement, this theory cannot account how the perturbation of a slow movement (which would increase the overall movement duration) can be corrected for on-line. It is possible that when the effector is perturbed a new τ-guide is initiated, although this would be difficult to establish. So while pre-setting the duration of an intrinsic τ-guide makes it computationally simple it suffers, like all feedforward models, from a lack of on-line prospective control that utilises expropriospecific information. That is, without a feedback mechanism movements cannot be updated on-line.

In its defence, it should be said that the τ-coupling theory is still in the early phases of development and will probably undergo further refinements. Once these have been made the extent to which this theory will be accepted as a rational explanation for movement control will depend on the degree to which it is deemed biologically plausible. Many scientists believe that the key to establishing the plausibility of a model of behaviour is to study correlates of the behaviour at a neurophysiological or biochemical level. Reduction is seen to hold the key to finding biological solutions to the problems of motor control. However, simply describing behaviour at a lower level does not constitute an explanation. A complete theory would need to account for the same behaviour at all levels of observation. That is, there is a need for theories to transcend different disciplines and demonstrate that phenomena observed at one level can be accounted for at another. At present the τ-coupling theory has only been explored at the behavioural level. The extent to which it is also likely to be able to account for what is known at the neurophysiological level is the topic of the next section.

## 2.4 Possible neural representations of τs and τ-couplings.

In order to start the process of assessing the τ theory in terms of its biological plausibility, a logical first step is to establish a framework in which to operate. Indeed, this has been the policy of many scientists involved in attempting to understand the neural basis of motor control. Many have restricted their studies to eye movements because studying the oculomotor system has several advantages over studying limb movements. For instance, since the rotations of the two eyes are controlled conjugately by twelve muscles, and the spinal cord is not involved in

their control, the degrees of freedom involved in the oculomotor system are drastically reduced compared to those in limb movements. Added to this eye muscles do not have a stretch reflex. As a consequence of this a great many studies have been undertaken on eye movements, and these have resulted in a detailed understanding of oculomotor physiology, and the proposal of numerous theories of motor control. This makes the oculomotor system, and in particular the saccadic system, an ideal candidate for assessing the biological validity of the $\tau$-coupling theory. It is important to note that the $\tau$-coupling theory addresses specific functions within the context of motor behaviour and it should not be thought of as an encompassing theory of neural function, however, if within this domain it is to provide a true explanation of aspects of motor control then it should account for the known neurophysiological findings better than alternative theories of oculomotor control.

Over the last three decades the functional specialisation of various populations of neurons thought to be involved in oculomotor control has been extensively studied using single cell recording and electrical stimulation techniques. These techniques have undoubtedly led to an increase in our knowledge of how the brain controls eye movements, but with the advent of neural network theories the utility of these paradigms has recently been questioned. For instance, Robinson who based his early work around the findings from single cell and stimulation studies now believes that

"the study of single neurons or neuron ensembles is unlikely to reveal the task in which they are participating or the contribution that they are making to it.

Conversely, even if one knows the function of a neural system, recording from single units is not likely to disclose how that function is being fulfilled by the signal processing of the neurons."

Robinson (1994) p43.

This view is seen as extreme by many, who, like Fuchs et al. (1994), support the notion that in some areas of the brain justifiable relationships between firing rates and sensory or motor events can be found. This, they believe, is especially true for the oculomotor system where neuronal firing rates have been found to correlate with movement parameters as for example, in the work on vestibular neurons of Melville Jones and Milsum (1971). By ignoring the neurophysiological data the neural network alternative runs the risk of providing a solution that bears no resemblance to what actually happens in the central nervous system. The use of back propagation has been criticised as being an unlikely candidate for self organising principles (Crick, 1989) and the problem of where the teacher of the network appears in the central nervous system or elsewhere, has still not been addressed.

If $\tau$-guides and $\tau$-couplings are not arbitrary concepts then they should be neurally represented. Since there is a considerable body of work which suggests the existence of neural oscillators (for example, Triesman et al., 1990, Gray and Singer, 1989, Pöppel, 1996) or neural clocks (for example, Buonomano and Merzenich, 1995, Ivry and Hazeldine, 1995) it would not be unreasonable to predict that there will be patterns of activity in the central nervous system that will be in agreement with the generalised $\tau$ theory. At present it is only possible to guess what form such

a representation would take, but Figure 2.1 shows a diagrammatical illustration of the firing pattern that would be expected for an intrinsic τ-guide if the inter spike interval at time t was proportional to the value of τ-guide at time t, $\tau_g(t)$ (based on personal communication from Lee 1997). It shows there to be a gradual build-up in firing frequency which then stops abruptly. The extent to which this pattern matches known discharge patterns, and possible areas in which such discharges might be found is discussed in the following section

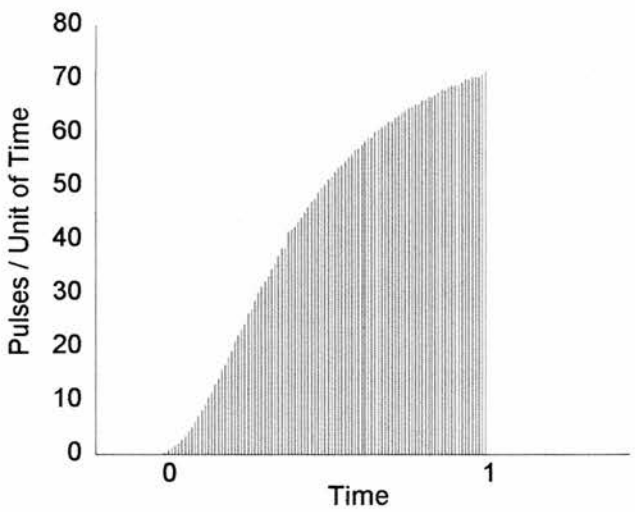



Figure 2.1 Schematic illustration of the firing pattern for a constant acceleration intrinsic τ-guide, assuming that the τ-guide start from rest at time zero and accelerates at a constant rate to reach its goal at time 1.

The assessment of τ theory outlined here involves comparisons being made with several areas of research which have established literatures. Since the τ theory is concerned with the temporal control of actions the first area to be considered is neural clocks and how time might be representation in the central nervous system.

Following on from this the literature pertaining to how gaps might be perceived is discussed, and possible mechanisms for the generation of an intrinsic τ-guide will be outlined. The nature of sensorimotor transformations is likely to be crucial in assessing the idea of τ-coupling, so the known physiological mechanisms involved in this will also be described. Finally, the theories of saccadic control and the implications they have for the theory will be commented upon.

## 2.5 The Representation of Time

The use of an intrinsic τ-guide suggests that the duration of a movement (T) can be accurately perceived or predicted. While there are many examples of skilled actions which require millisecond timing precision, the existence within the central nervous system of an internal clock that constructs or counts in real time is a matter of great debate. Since many experiments have shown that subjects can perform tasks with remarkable temporal accuracy and consistency there is a general belief that humans have an internal reference clock (for example, Ivry and Hazeldine, 1995, Pöppel et al., 1996). There is also some compelling evidence to suggest that this clock does not always run at the same rate. The review by Wearden and Penton-Voak (1995) of the studies carried out over the last fifty years on the effect of body temperature on the rate of subjective time shows that the internal clock is temperature sensitive (time passes faster as temperature increases). Raising stress levels seems to have a similar effect (Boltz,1991) and the temporal distortions experienced by Parkinson's patients have led some to suggest a possible dopaminergic mechanism for subjective time estimates within the basal ganglia

(Pastor et al., 1992, Wogar et al., 1993).

Other areas of the brain have also been implicated in timing, the work of Wang and Frost (1992) indicated that cells in the nucleus rotundus of the pigeon code temporal information, or rather time to contact, and of course the role of the cerebellum should not be overlooked either. Observations of patients with cerebellum damage indicate that this part of the brain has a vital role in the temporal co-ordination of movement. Cortical structures also appear to be important in motor timing, right precentral damage leads to an overestimation of temporal intervals, while left precentral damage leads an underestimation (von Steinbüchel et al., 1996). However, the perception of 'non-motor time' is frequently preserved following cortical damage (Halsband et al., 1993, Shaw and Aggleton 1994) which suggests that the temporal aspects of perception and action may be represented independently

This research indicates that the representations of perceptual, movement and intrinsic τs are likely to be multiple and widespread within the central nervous system, and it raises the question of whether movement time is constant in relation to clock time. Any internal clock involved in the generation of τ-guides might be expected to slow down or speed up when core temperature fluctuates in times of stress, as subjective time does.

## 2.6 Maps and Gaps

τ is a measure of time, and cannot differentiate between different spatial locations. Yet the τ-coupling theory is concerned with the closure of gaps, whether

it be in terms of distance, angle or force, which means that there is also a spatial and energetic dimension to the theory. Consequently, if biological plausibility is to be sought then it will be insufficient to just look at how the central nervous system's internal clocks function. It will also be necessary to look at how, or indeed if, spatial or energy time gaps are neurally represented

The human brain has many areas which are topographically or somatotopically mapped. Thus, activity in one particular area of such a brain map correlates with the happenings in one spatial location in the body or the world. This function means that physical gaps in relation to the body relate to neural maps. It is conceivable, therefore, that when a gap is closed, the $\tau$ of that gap will relate to the firing rate of neurons at a particular location on a map

The relationship between $\tau$-coupling and topographical mapping is important since it provides a means of perception-action coupling. The writings on $\tau$ (Lee and Reddish, 1981 and Lee et al., 1983) described situations where simple and direct couplings appeared to exist, but as the literature in this field has grown it has becoming increasingly apparent that most situations involve the integration of multiple sources of sensory information. Many believe that an understanding of how the brain perceives and integrates these numerous sources of information is still a long way off, but there are some who believe that they have the basis of an answer. One such scientist is Edelman who proposed the theory of neuronal group selection (Edelman, 1987). The validity of this theory is still a contentious issue, but it does provide a possible way in which ecological theories of perception and action can be conceived of as 'working' at a neural level.

Edelman's theory has three basic elements; neuronal group selection, reentry and global mapping. Neuronal group selection is concerned with how the anatomy of the brain emerges, while reentry tries to explain how experiences create patterns of responses. Finally, global mapping describes how signalling between maps could give rise to behavioural functions

The idea of reentrant signalling relies on the premise that maps are functionally segregated but connected by massively parallel and reciprocal connections. So, when groups of neurons on one map are selected, other groups of neurons on different maps are also selected since they are 'reentrantly connected'. Edelman goes on to propose that

"Not only are events correlated topographically across different maps without a supervisor, but new selectional properties emerge through successive and recursive reentry across maps in time..... Perceptual categorisation occurs by coupling the outputs of multiple maps that are reentrantly connected to the sensorimotor behaviour of the animal. A global mapping is a dynamic structure containing multiple reentrant local maps (both sensory and motor) that are able to interact with non-mapped parts of the brain. "

Edelman, (1992) p89

In terms of τ-coupling the three different forms of τ (perceptual, motor and intrinsic), could form a global mapping while the cerebellum and basal ganglia, the structures that Edelman calls the 'organs of succession', could be fundamental in the processes of coupling. To talk of τ theory in terms of neuronal group selection

might be appealing to ecological psychologists, but might also be premature since Edelman's theory is far from accepted. The existence of neuronal groups has been questioned (Crick, 1989, Barlow, 1988), and his claims that neuronal groups undergo a Darwinian-like selection is widely disputed. It is far from clear how Edelman's version of synaptic strengthening can be seen to operate in a manner that is similar to Darwin's notion of inheritance, however, his ideas provide a way of thinking about how activity on multiple maps might result in an integrated response. The following sections deal more precisely with how the saccadic system might do this.

## 2.7 Perceiving Gaps

As previously stated, in order to close a gap using $\tau$-coupling the changing nature of the gap must be perceived. One likely site for the representation of spatial relationships between objects in the world and the body is the posterior parietal cortex (Stein, 1994). Sensory information from the retina reaches the posterior parietal cortex via striate and prestriate cortices, and this area also receives vestibular, auditory inputs as well as inputs from the midbrain and cerebellum. Furthermore, projections from the limbic and reticular systems to the posterior parietal cortex indicate that a motivational element is also involved

The multiple sources of sensory information feeding into the posterior parietal cortex indicate that this is an important area for perception of gaps, and in particular gaps which are defined visually. An inability to visually attend to environmental stimuli is commonly seen following parietal lesions (Pohl, 1973, Petrides and Iversen, 1979), and further evidence for how information is represented

in this area comes from the discovery of three behavioural classes of neuron found in area 7a; visual fixation neurons (Mountcastle et al., 1975), tracking neurons (Sakata et al., 1983) and saccade neurons (Lynch et al., 1977).

Visual fixation neurons receive inputs from the fovea, but almost all tracking and saccade neurons, that fire in association with eye or hand movements, receive visual inputs from the periphery. These movement related neurons respond weakly to stationary stimuli, but making an eye or limb movement towards a target, or simply shifting one's attention to it, increases the neuronal firing rate (Bushnell et al., 1981, Robinson and Peterson, 1984, Goldberg and Bruce, 1985). While these neurons do not encode speed, they are sensitive to motions away from (centrifugal), or towards (centripetal) the midline (Motter et al., 1987), and are thought to be important in the representation of optic flow patterns (Motter, 1991). These findings fit well with the concepts of $\tau$-coupling and the idea that movement $\tau$s give rise to perceptual $\tau$s.

The posterior parietal cortex is not the only area which is of interest in relation to optic flow patterns, since there is a growing body of evidence suggesting extrastriate areas with large receptive fields, and in particular neurons in the dorsal medial division of the medial superior temporal area (MSTd) respond selectively to optic flow (Wurtz and Duffy, 1992). Cells in the MSTd region are sensitive to single types of motion (inward or outward radial motion) as well as more complex motions with multiple rotations. The complexity of the functions of different cells seem to suggest that the representation of a gap is more likely to involve a system rather than cells in any one particular region.

The possibility that time to contact is neurally represented became more of a reality with the publication of data by Wang and Frost (1992). They ran an experiment in which pigeons were presented with a looming stimuli that signalled a head-on collision. They recorded the activity of neurons in nucleus rotundus and found a sub-population of neurons that selectively responded to the $\tau$ of the looming stimulus. This data provided strong evidence to suggest that time to contact is both perceived and neurally represented.

## 2.8 Choosing an intrinsic $\tau$-guide

To close a gap using a coupling that involves an intrinsic $\tau$-guide an appropriate guide needs to be 'chosen' (that is an estimate of the guide's duration has to be made), and the strategy to be used (defined mathematically as the value of the coupling constant k) needs to be decided upon. These decisions are not only based on postural restraints, but also on what the person intends to do upon arrival. It seems likely that the selection of a guide for an eye movement would require the involvement the frontal cortex and the cerebellum.

Traditionally, the frontal eye fields have been thought of as being the motor cortex for voluntary ocular movements. Ferrier (1874) was among the first to observe that stimulating the frontal lobes elicits contralateral eye movements. More recently Bizzi and Schiller (1970) found that the cells in the frontal eye fields discharged during saccadic movements. Furthermore, Bruce et al. (1985) found that stimulating the ventrolateral (more central) region produced small movements, while the dorsomedial (more peripheral) portion elicited large saccades. Since the size and direction of the movement are dependent upon the site of stimulation, the frontal eye

fields are said to be topographically mapped

The role of the frontal eye fields in saccadic control is complex and subtle. In humans, lesions to the frontal lobes cause difficulties in making voluntary contralateral saccades as well as in suppressing unwanted saccades (Daroff and Hoyt 1971, Guitton et al., 1982), but they do not abolish saccades. They seem to be important for the initiation of purposive movements, which implies that the control of non-purposive movements is elsewhere. Indeed Schiller et al.'s 1980 finding that only with the bilateral destruction of the frontal eye fields and superior colliculus is there an inability to generate saccades, suggests that in the monkey two parallel pathways are involved. It is now generally believed that the frontal eye fields pathway is concerned with 'cognitively driven' saccades, while the pathway via the superior colliculus is concerned with faster 'orienting responses'. Thus, it could be proposed that the frontal eye fields will be involved with the choosing or implementation of intrinsic $\tau$-guides, and the superior colliculus with the coupling of perceptual and motor $\tau$s. However, to date, the single cell recordings from the superior colliculus do not match with those predicted for a $\tau$-guide if $\tau$ is proportional to the interspike interval (see Figure 2.1), and it is likely that if these processes exist they will be distributed.

For well practised actions choosing an intrinsic $\tau$-guide is likely to be based on memories of previous actions. Motor memories are thought to reside in the cerebellum (Ito, 1984), and as Stein and Glickstein (1992) point out, there are five major types of theories of cerebellar function; a comparator, a timing device, a parameter adjuster, a predictor and a learner. In humans, damage to the cerebellum causes a variety of dysfunctions. Damage to the midline results in problems with

posture, gait and the vestibulo-ocular reflex, whereas damage to the hemispheres disrupts the control of voluntary limb and eye movements. Evidently, the cerebellum is a critical structure for the control of action, and it could be a possible site for the coupling of various perceptual, sensory and motor τs. This is discussed in greater length in Chapter 5 where a study of the role of the cerebellum in τ theory is made.

## 2.9 Movement τs.

Once an intrinsic or extrinsic τ-guide has been established, a movement τ must be generated that couples onto this dynamic prototype. Two of the areas of the brain which are likely to be involved in the generation of a gaze-movement τ are the superior colliculus and the oculomotor neurons of 'pulse generator' in the midbrain tegmentum. Since these areas are involved with 'coding' the output signals sent to the muscles they seem to be likely candidates for the neural representation of a movement τ and the coupling between perceptions and actions.

## 2.10 τ-coupling and the Superior Colliculi

The superior colliculi are laminated structures situated at the top of the midbrain. The three most dorsal layers (the superficial superior colliculus) form a visual sensory structure, while the four ventral layers (the deep superior colliculus) are primarily thought of as a motor structure. However, many cells in the deep layers also have visual receptive fields and since some of these 'visual' neurons are also known to be involved in the control of visually guided saccades they appear to

have both perceptual and motor functions. Like the frontal eye fields the superior colliculi are topographically organised, and the telotopic map in the superficial superior colliculus of the monkey represents the contralateral visual field that subtends from zero to eighty degrees

There is an extensive literature on the relationships between gaze shifts and various discharge patterns of cells in the superior colliculus. In his summary of this work Guitton (1991) proposed four different characteristic discharge patterns: sensory evoked bursts, low frequency activity following sensation, low frequency activity that precedes motor activity, and high frequency bursts that precede movement.

Interestingly, different classes of neuron in the superior colliculus have been found to respond to different stimuli. For instance, visually triggered neurons (VTMN), as their name suggests, discharge prior to visually triggered but not spontaneous saccades (Mohler and Wurtz 1976). Saccade related burst neurons (SRBN) on the other hand, do not fire in relation to sensory stimuli but fire prior to and during the movements (Jay and Sparks 1987). Overall, various discharge patterns from superior colliculus neurons have been linked to four different categories of saccades; spontaneous, visually driven, auditorily driven, and cognitively driven. Understanding how the firing patterns of these various neurons relate to movement $\tau$s could provide valuable insights into how, or if , temporal gap information is neurally represented.

There are two groups of neurons found in the deep layers that appear to be particularly important for perceptuo-motor control; tecto-reticular neurons (TRN) and tecto-reticulo-spinal neurons (TRSN), collectively known as TR(S)Ns.

Recording from single TR(S)Ns in the superior colliculus of the cat, Munoz et al. (1991b) demonstrated that these neurons are also organised to form a somatotopic map. Initial findings indicated that the locus of activity on this motor map prior to a movement onset specifies the gaze-target gap, the so called gaze error. Guitton (1992) went on to hypothesise that during a saccade the locus of activity in orienting neurons (oTR(S)Ns) moves rostrally across the map until cells in the fixation zone (fTR(S)Ns) are activated. This is schematically illustrated in Figure 2.2. The locus of activity on the map relates to the size of the gap, and the extent of the activity (a function of the number of active neurons and their discharge frequencies) influences saccade velocity.

Since TR(S)Ns project contralaterally to the eye and head motor centres in the brain stem, this moving wave of activity across the superior colliculus has been implicated in the transformation of spatially organised neural activity into a temporal code that is utilised by motoneurons (Guitton, 1992). It could also provide a mechanism by which a temporal representation of a gap is 'converted' into a movement $\tau$ which will physically close the gap. However, recently the theory linking a caudal-rostral wave of discharge moving through the tectal of the deep superior colliculus to the movement dynamics has been questioned by the neural network theorist, Moschovakis (1996). He pointed out that the moving hill theory predicts that build-up cells (cells which discharge prior to a movement) will be sequentially activated during a movement, starting from the caudal regions and moving rostrally. Recording from monkeys, Munoz and Wurtz (1995) found that all build-up cells are activated at the onset of a saccade, and Moschovakis argues that these activation patterns are not clearly related to the time course, or the spatial

distribution, of discharge patterns of the long lead burst neurons that connect the superior colliculus to the burst generators. This casts some doubt on the idea that there is a direct relationship between a moving wave and movement dynamics and suggests that the dynamics of a movement are more likely to have distributed representations. Evidently further work is needed to unravel this.

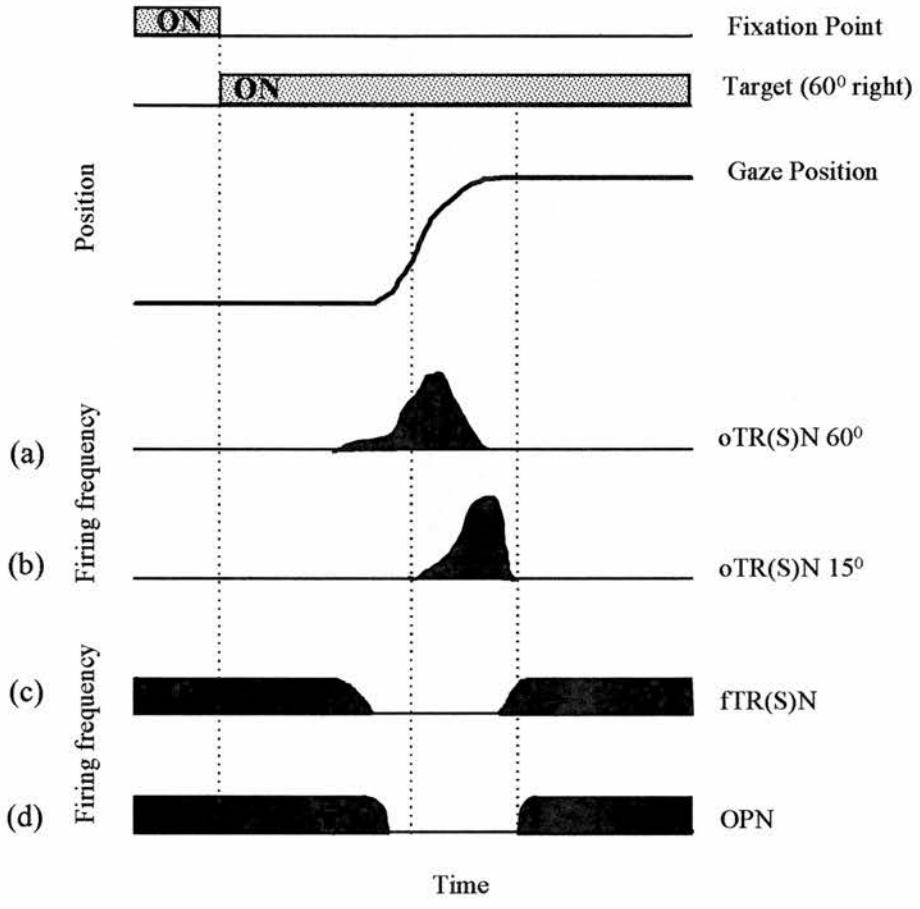



Figure 2.2 Diagram illustrating discharge patterns of various neurons during a gaze shift in a cat. Panels (a) and (b) show the discharge patterns of two orienting TR(S)Ns at different positions on the telotopic map, while panel (c) depicts activity in a fixation TR(S)N. It should be noted that as the gaze shift progresses there is a shift in the temporal pattern of activity across the map. Panel (d) shows the firing pattern of an omnipause neuron (OPN). Taken from Munoz et al. (1991b).

Despite the complexities of this structure, behavioural characteristics associated with TR(S)Ns activity seem to be emerging that are important for the $\tau$ theory. For example, the appearance of a visual target just prior to movement onset causes a sudden change in the acceleration of the gaze to occur during the gaze shift, and a corresponding increase in oTR(S)N discharge frequency (Munoz and Guitton, 1989, Guitton et al., 1990). The acceleration of the gaze was found to start approximately 50 milliseconds after the appearance of the target, and since the fastest reaction times in monkeys were previously thought to be in excess of 70 milliseconds, Munoz and Guitton concluded that the visually evoked changes in TR(S)Ns that corresponded to the appearance of a target in the neuron's visual field, had triggered the motor command. This explanation implies a direct perception-action coupling. The discovery of fast conducting Y-cell axons that project monosynaptically from the retina to the TR(S)Ns (Berson and McIlwaine, 1982, Beckstead and Frankfurter, 1983) provides a mechanism which could account for this coupling. Ultra fast responses to visual stimuli have also been reported in cats (e.g. Pettersson et al., 1997) and the cortico- and rubrospinal tracts have been implicated in these actions.

By stimulating the intermediate and deep layers of monkey superior colliculus Freedman et al. (1996) have helped to clarify the complex relationships between the locus and extent of activity in the superior colliculus and metrics of gaze movements. They found that varying the intensity and frequency of stimulation at a particular site on the superior colliculus influenced the gaze velocity but not the gaze amplitude. When the activity level was high (high frequency or high current level) time to contact was reduced, whereas when the level was low time to contact

increased. They concluded that the level of collicular activity influences movement dynamics but not displacement.

The amplitude of the gaze movement was found to be related to both the site and duration of stimulation. The locus of the stimulation defined the maximal possible movement, but sub-maximal movements were found to occur when the duration of stimulation was reduced. Stimulating at any one particular site could produce movements of all amplitudes, up to the site defined maximum. Surprisingly, the dynamics of the sub-maximal movements mimicked those of visually guided saccades. For example, a short duration stimulation at a caudal site that had a maximum gaze amplitude of forty degrees, produced a ten degree movement that had a similar peak velocity to that of a ten degree visually guided saccade. The visually guided saccade however, would have started from a different location on the map. In other words truncated movements at caudal sites mirrored the kinematics of movements originating from more rostral sites. This finding led them to conclude that collicular activity at any site initially drives gaze along a similar amplitude/velocity curve. They went on to show that the contribution of the head movement to the gaze shift was dependent upon the orbital position of the eye, and supported the notion proposed by Phillips et al. (1995) that the superior colliculus sends a single gaze command to separate head and eye controllers, that is it is telotopic.

These findings pose some problems for the $\tau$-coupling theory. Firstly, the discharge patterns seem to be related to velocity and not $\tau$, although it must be said that no-one has ever correlated discharge patterns with $\tau$. Secondly, there is a problem with the finding that collicular activity at any site initially drives gaze along

a similar amplitude/velocity curve since it implies that the initial rate of acceleration will be constant. However, changing the value of the coupling constant in the τ-coupling equation changes the shape of the gaze velocity profile, (as shown in Figure 1.1) and the initial rate of acceleration. Finally, Freedman et al.'s (1996) results imply that the gaze movement τ must be composed of, or decomposed into separate head and eye τs each having different onsets, offsets and durations. While this may not be a problem as such, exactly how this is done is not stated in the τ theory.

## 2.11 The Saccadic Pulse Generator and the Representation of Movement τs.

The superior colliculus may be involved with the coupling of various τs, but it is the burst generator in the brain stem which is the most likely candidate for the representation of movement τs. During a saccadic eye movement there is a high frequency burst of activity in the agonist ocular muscle. Once the eye has reached its goal the motoneurons of the agonist muscle assume a new higher level of tonic innervation so that the new position is maintained. This pulse-step pattern of innervation seen in the extraocular muscles is mirrored by activity in the brain stem, and in particular the pontine paramedian reticular formation (PPRF). Single cell recordings from the PPRF have revealed three types of cells; burst, omnipause and position neurons. There are two types of burst neurons that fire just prior to and during a saccade; long lead (LLBN) which start to fire approximately 100ms prior to the movement and short lead (SLBN) which start to discharge about 80ms later. It has been suggested that LLBN provide an excitatory input to SLBNs and these

project to the ocular motor neurons (Luschei and Fuchs, 1972). The pulse of activity in the agonist muscles has been found to be closely associated with SLBN activity. The duration of SLBN firing has been found to be nearly identical to the duration of the saccade, and the firing rate equivalent to the instantaneous eye velocity. Furthermore, the total number of spikes in the burst has been found to be proportional to saccade amplitude (Henn and Cohen, 1976, Hepp and Henn, 1979, Keller et al., 1974, van Gisbergen et al., 1981).

Tightly coupled to the firing of SLBNs, is the firing pattern of the omnipause neurons. During fixation these cells have high tonic firing rates, but they are completely silent during saccadic movements. It is during the cessation of omnipause activity that a saccade occurs. When a saccadic movement is not taking place the firing of omnipause neurons is thought to inhibit SLBNs, functionally disconnecting them from the saccade generating circuitry (King and Fuchs, 1977). Once the pulse of activity is over, firing is observed in eye position related neurons (EPRN). These neurons are thought to be part of the neural network that integrates the pulse signal from the SLBN to a fixation signal, the so called 'neural integrator' (Strassman et al., 1986, Schall, 1991). As yet, little is known about the transition from the pulse to the steady state and the neural units responsible for coupling these two distinct phases together have not been identified. Collectively, the saccade related neurons in the brain stem are known as the 'saccadic pulse generator', and the activity they exhibit is dependent upon the signals received from other parts of the brain. It seems unlikely that the input to these neurons only relates to the specifics of a movement $\tau$ ($\tau_{GT}$) since the discharge patterns of the SLBN, omnipause and position neurons do not correspond to the time constraints of a

movement τ. However, this is not to say that the neural representation of τ in the paramedian pontine reticular formation should be ruled out, but it does indicate that other control mechanisms and parameters also need to be considered.

## 2.12 Theories of Saccadic Control

τ theory is fundamentally different to the established theories of oculomotor control especially in terms of the nature of control parameters and the way in which feedback is used. Many of the models of gaze saccades that have been developed over the last three decades have been inspired by the Robinson model (1975). He proposed that a local feedback loop receives a signal that represents initial motor error. This signal is converted into a pulse of activity which specifies the amplitude and velocity of the saccade and is sent to the motoneurons. The effect that this pulse of activity has upon eye position is monitored internally by integrating the pulse frequency to give an estimate of the current displacement of the eye. This estimated displacement is then compared to the desired displacement, and as long as these are unequal activity in the burst generator continues to move the eye.

As this basic idea gained in popularity the possible contributions of retinal information and signals from the extraocular muscles were largely dismissed, although it is now recognised that these can be important sources of information (Hayman et al., 1995). It is generally believed that saccadic eye movements are pre-programmed and 'ballistically' controlled using an efference copy within a local feedback loop.

To date there are essentially two main classes of gaze control models; those in which the superior colliculus functions in an open loop fashion, that is it only

specifies the initial vector of eye motor error, and those in which the superior colliculus is within a feedback loop and specifies instantaneous motor error. However, both kinds of models have the same four basic ingredients namely a sensor, a controller, a plant and a feedback loop. The sensor measures the error between the target and the eye in space while the controller converts the sensory signal into a motor command. The plant executes the motor command by producing a motor output that causes a change in eye position, and the negative feedback loop monitors the progress of the on going movement by integrating the eye velocity signal being sent to the oculomotor muscles, and comparing this estimated displacement to the desired displacement.

In comparison, the τ-coupling theory has elements of both feedforward and feedback control. The use of an intrinsic τ-guide which is pre-set and cannot be updated implies a feedforward control mechanism, yet the use of an extrinsic τ-guide implies on-line prospective control based on feedback. Instead of having a rigid system that only allows for one kind of control mechanism, τ theory allows for the use of either depending on the nature of the task and the perceptual information available.

Like the systems theories, the τ-coupling theory uses some form of comparator mechanism to monitor couplings, and utilises stored motor memories when choosing strategies. Unlike these models though, the τ-coupling theory appears to be more parsimonious in that it does not need a neural integrator. Unfortunately, it does not provide an alternative role for caudal pons, the proposed site of the neural network that integrates the vestibular velocity signal into an

oculomotor position signal (Arnold and Robinson, 1991). This suggests that non τ like information, that is not perceived directly, plays an important role in oculomotor control.

The various models of saccadic control are discussed further in Chapter 4, but it is evident from the above that there are significant differences between the systems models and the τ-coupling theory. In light of this, further work is needed to clarify the role of the τ theory in gaze control.

## 2.13 Assessing the plausibility and generality of the τ-coupling theory.

On the basis of the literature reviewed it would seem that the biological plausibility and generality of the τ-coupling theory need to be assessed. To establish that this theory has a high degree of generality it would be necessary to demonstrate τ-couplings in a variety of movements, and in particular gaze shifts and reaching movements. A first step towards establishing the possible mechanisms involved in τ-coupling and the role various brain structures play in τ-coupling could be assessed by studying patients with brain damage.

A series of experiments were undertaken to investigate these two criteria. The first (Chapter 4) is concerned with the control of gaze shifting, the aim being to investigate the nature of τ-coupling in these movements and to assess if the τ-coupling data is congruent with previous models of oculomotor control. The second series of experiments (Chapter 5) considers the role of the cerebellum in τ-coupling, by studying the behaviour of an adult with cerebellar damage. Finally, the third experimental series (Chapter 6) investigates the generality of τ-coupling in reaching movements.

# Chapter 3 : General Methods

## 3.1 Data Collection

A Selspot I movement registration system was used to capture head and limb movements. This is an opto-electrical device that uses infra-red sensitive cameras to track infra-red light emitting diodes (IRLeds). Measurements were made of movements that were primarily two dimensional and details of camera positions are given in the methods sections of each experiment. All data were sampled at 312Hz, converted from an analogue to a digital signal and stored on an Archimedes computer.

Eye movements were recorded using electro-oculography and this signal was pre-amplified and captured through an analogue channel of the Selspot system. This allowed measures of head, eye and target movements to be synchronised.

## 3.2 Data Analysis

Data analysis programmes were either written in Archimedes Basic and run on an A3020 Archimedes computer or in Kaleidagraph a PC based analysis and plotting programme.

### 3.2.1 Filters

Table 3.1 shows the various filters and cut-offs that were used in the experiments. The Gaussian filter used for the finger movements in Chapter 5 was

used so that direct comparisons with data from a previous experiment could be made.

| | Movement | Low Pass Filter | Cut-Off Freq (Hz) |
|---|---|---|---|
| Chapter 4 | Eye | Low pass analogue | 100 |
| | Head | 4th order Butterworth | 12 at -3dB |
| | Target | 4th order Butterworth | 12 at -3dB |
| Chapter 5 | Finger (reaching) | 4th order Butterworth | 8 at -3dB |
| | Leg | 4th order Butterworth | 8 at -3dB |
| | Eye | Low pass analogue | 100 |
| | Head | 4th order Butterworth | 12 at -3dB |
| | Target | 4th order Butterworth | 12 at -3dB |
| | Finger to mouth | Gaussian | sigma 32ms |
| Chapter 6 | Finger | 4th order Butterworth | 8 at -3dB |
| | Head | 4th order Butterworth | 8 at -3dB |
| | Target | 4th order Butterworth | 8 at -3dB |

Table 3.1 Summary of filters used.

### 3.2.2 Calculating Movement τs

The movement τ of a gap was calculated by dividing the distance or angle to the desired goal by the velocity of approach. The start of a movement was defined as the point at which the gap velocity first became non-zero and the end of the movement was defined as the time at which the gap velocity returned to zero.

Since the measurement of τ is noisy at low velocities some data were removed from subsequent analyses. Since it was desirable to remove only a minimal amount of data different criteria were used for different movements. For eye movements the accepted protocol found in the literature was used. This is a cut-off of data below 30 deg/sec and is used since small fluctuations in eye movements are noted even when a subject maintains a fixed gaze. Therefore, once τ had been

calculated for the whole movement, data below the 30 deg/sec cut-off was removed. Typically, this corresponded to two or three data points, that is less than 10ms.

Head movements with an angular velocity of less than 10 deg/sec and leg movements below 10 deg/sec (Experiment 5.6) were not included. For reaching movements, data where gap velocities of less than 1cm/s were ignored, while the hand movements made in Experiment 5.8 a cut-off of ten percent of peak velocity was used. The latter criterion was used so that the results would be comparable to previous experiments.

### 3.3.3 Intrinsic τ-guides

Intrinsic τ-guides were calculated for the whole movement duration using the following equation :

$$\tau_g(t)=0.5((t-T^2)/t) \qquad (3)$$

where T equals the total duration of the movement, and t is a time series starting at movement initiation and ending at contact.

### 3.2.4 Assessing τ-couplings

To test the τ-coupling hypothesis it is necessary to determine how closely the data satisfies the coupling equation $\tau_x = k\tau_y$ described in Chapter 1. This entailed computing the coupling constant, k, assessing the strength of the coupling, that is measuring the straightness of the line created by plotting $\tau_y$ against $\tau_x$, and the

duration of the coupling, that is the percentage of the movement for which the $\tau_y$ against $\tau_x$ line was straight.

3.2.5 Computation of k

The value of k which yielded the best line fit over the time interval ($t_s$, $t_e$) was computed from the equation

$$S = \sum_{t=ts}^{t=te} [\tau_m(t)-0.5((t-T^2)/t)]^2 \qquad (4)$$

where S is the sum of squares of the deviations of the movement data, $\tau_m(t)$, from the values, $k\tau_g(t)$, predicted by the hypothesis. T equals the total duration of the movement, $t_s$ the time at which the guide starts, and $t_e$ the time at which the guide ends.

The line of best fit is when S is minimum, i.e. when $\frac{dS}{dk} = 0$ or

$$- \sum_{t=ts}^{t=te} [\tau_m(t)-0.5k((t-T^2)/t)]\ ((t-T^2)/t)$$

$$= \sum_{t=ts}^{t=te} \tau_m(t)((t-T^2)/t) + \sum_{t=ts}^{t=te} 0.5k((t-T^2)/t)^2$$

$$= 0 \qquad (5)$$

Thus, solving for k,

$$k = \frac{\sum_{t=ts}^{t=te} \tau_m(t)(t-T^2/t)}{\sum_{t=ts}^{t=te} 0.5\,(t-T^2/t)^2} \qquad (6)$$

3.2.6 Assessment of τ-coupling strength

This procedure was used to assess the linearity of the plot of $\tau_y$ against $\tau_x$. Using the least squares model (Hays, 1963), $r^2$ was computed as follows :

$r^2$ = 1-sample variance of estimate for standard scores

$$= 1 - \frac{\sum[\tau_m(t)^* - k\tau_g(t)^*]^2}{N} \qquad (7)$$

where

$$\tau_m(t)^* = \frac{\tau_m(t) - \text{mean}\,(\tau_m(t))}{\text{s.d.}\,(\tau_m(t))}$$

$$k\tau_g(t)^* = \frac{k\tau_g(t) - \text{mean}(k\tau_g(t))}{\text{s.d.}(k\tau_g(t))}$$

N= number of samples

3.2.6 Assessing the duration of a τ-coupling

(a) Regression Technique

$\tau_y$ was plotted against $\tau_x$ and taking the last 10 data points in this series a linear regression line was calculated. The standard deviation, $S_{10}$ , of the points about the regression line was determined using the formula

$$S_{10} = (1-r^2) \qquad (8)$$

Moving backwards through the data from the point end-11 to the start, the relative deviation of each point from the regression line was calculated using the formula

$$D_n = \text{distance of point from regression line} / S_{10} \qquad (9)$$

The relative deviation was then plotted against time, and the time at the first data point with a relative deviation of below two was noted. Provided that the $r^2$ value was $\geq 0.96$, this point was taken as the start of coupling. In Experiment 5.6 slightly different parameters were used, the start of coupling was defined as the point at which the relative deviation dropped below 3, provided that $r^2$ value was $\geq 0.97$. Again this was done to make the results comparable to a previous study. Finally, the number of points in the straight section divided by the total number of points included in the analysis gave a measure of the percentage of the movement time for the τ-coupling.

(b) Bland Altman Method of Agreement

The use of correlation in determining the degree of relationship between two variables has been criticised since it is dependent upon the sample range (Bland and Altman, 1986). An alternative form of assessment is to estimate the degree to which two quantities are in agreement and this can be done using the Bland Altman method of agreement. This technique was also used to estimate the time of coupling onset for the data in gaze shifting experiment in Chapter 4. $k\tau_y$ was deemed to be in agreement with, that is coupled to $\tau_x$ when the mean difference between the two lay within two standard errors. This is illustrated in Figure 3.1

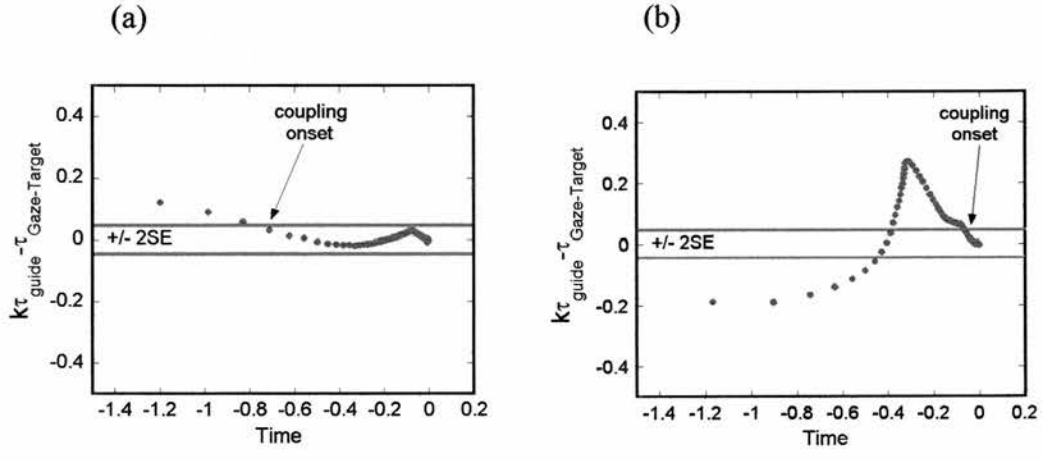



Figure 3.1 Bland Altman plots for two trials indicating an early onset (a) and late onset (b) of $\tau$-coupling.

On all but 5 trials (n=379) the results from the regression technique and the Bland Altman differed by less than 2 percent. Therefore, on the experiments in Chapters 5 and 6, only the regression technique was used.

# Chapter 4 : τ-Coupling and the Control of Gaze Movements

## 4.1 Introduction

The τ-coupling theory proposes that sensory information entering the brain is perceived as the τ of a gaze-target gap. Movements which change the physical gap are mirrored by changes in the perceptual representations of that gap. Thus, movement τs are coupled to perceptual τs. The controlled closure of the gap can be brought about by keeping the ratios of a combination of self generated τ-guides, perceptual τs and motor τs constant. Implicit in this theory is the idea that τ information provides the basic substrate for all neurological control mechanisms. Sensory organs relay τ information to the brain where an assessment of the required coupling is made prior to the appropriate τ information being sent to the muscles.

There are two fundamental differences between the τ-coupling theory and the systems theories of saccadic control. First, the control mechanism proposed by the systems theories involves a local feedback loop and a neural integrator that integrates eye velocity information so that the current displacement can be compared to the desired displacement. The τ-coupling theory on the other hand proposes that control is achieved by perceiving and coupling τs. Second, the τ theory is ecological in nature and asserts that, given sufficient time, gaze shifts can be prospectively controlled using expropriospecific information picked up during the movement. In contrast the systems models propose that saccades are pre-

programmed ballistic movements during which retinal information, or information from the extraocular muscles, is not utilised.

### 4.1.1 Is visual information suppressed during saccades ?

During a saccadic eye movement there is no perception of the world being blurred. Likewise, when looking in a mirror it is not possible to see the eyes move during rapid refixations. As a result of these general findings and those by Holt (1903), Volkman (1962), and Latour (1962), amongst others, it is generally believed that vision is actively suppressed during saccades. However, recently several experimenters have shown that useful visual information can be picked up during these fast movements, and that it can in some instances be used to modify ongoing or subsequent movements.

In a series of experiments by Burr and colleagues (Burr et al., 1982, Burr et al.,1994) in which they manipulated the spatial frequency, colour and luminance contrast of patterns it was found that patterns with high spatial frequency, or equiluminance, were not suppressed during saccades. Similarly, Ilg and Hoffman (1993) demonstrated that subjects were able to perceive intrasaccadic movements of an object independently of retinal slip, and they suggested that saccadic suppression is related to delayed central processing of retinal information during saccades. This explanation also fits the data of Deubel et al. (1996) who conducted some experiments that indicated that the sensitivity to the displacement of a target during a saccade was enhanced when the target is blanked out at the end of the saccade. Furthermore, Prablanc and Martin (1992) demonstrated that subjects were

able to accurately point to a target that had been displaced during a saccadic movement even though they did not report seeing the target move.

Together these data suggest that it is not the case that all visual information is unavailable during saccades, but rather that the perception of this information is somewhat degraded and the inherent time delays are such that it cannot be acted upon. It seems logical to assume that saccades are pre-programmed and most of the models of saccades are based on this assumption, yet, there is evidence to show that this assumption is not always correct. Hallett and Lightstone (1976) demonstrated that visual information gained during a saccade could be used to programme certain characteristics of subsequent saccades. Moreover, Zee et al. (1976) demonstrated that in certain circumstances saccadic movements could undergo on-line modifications. They studied two patients who had slow saccades as a result of spinocerebellar degeneration, and using a paradigm in which the target jumped during a saccade they found that these subjects were able to modify their response during the saccade so as to hit the target in its new position. They concluded that these patients could continuously receive visual information, even when their eyes were moving, and use this to appropriately modify their eye movements mid-flight. This finding suggests that during long duration gaze shifts healthy humans should, in theory, be able to control gaze shifts prospectively. The first aim of this experiment is to see if this is the case.

### 4.1.2 Models of Gaze Control

One of the most interesting problems in oculomotor control has been to try and understand how the spatial and temporal output signals from the superior

colliculi are 'transformed' into the temporal discharge that is required by the motor neurons associated with the ocular muscles. As discussed in Chapter 2 most of the original models of this circuitry placed the pulse generator inside a local feedback loop. These systems models propose that the burst element receives a signal representing the initial motor error, and this was converted into a pulse of activity the characteristics of which determine the amplitude and velocity of the movement. During the saccade an estimate of the eye's position was obtained by integrating the eye velocity signal being sent to the oculomotor muscles, and the progress of the saccade was monitored by comparing this estimated displacement to the desired displacement. As long as they were unequal the burst generators continue to fire.

Several revision to the early models have been made, and more recent models have placed the superior colliculus within this loop (for example, Munoz and Guitton, 1989, Galiana and Guitton, 1992). Figure 4.1 illustrates one such model. This model suggests that the superior colliculus is involved in a spatial-temporal translation, but by placing it within a local feedback loop the model implies that the superior colliculus receives an initial motor error signal that is not updated on the basis of visual information. In order for the saccade to be accurate, a true representation of the target in egocentric space is a necessary precursor since retinal information or information from the extraocular muscles cannot be used to guide the movement.

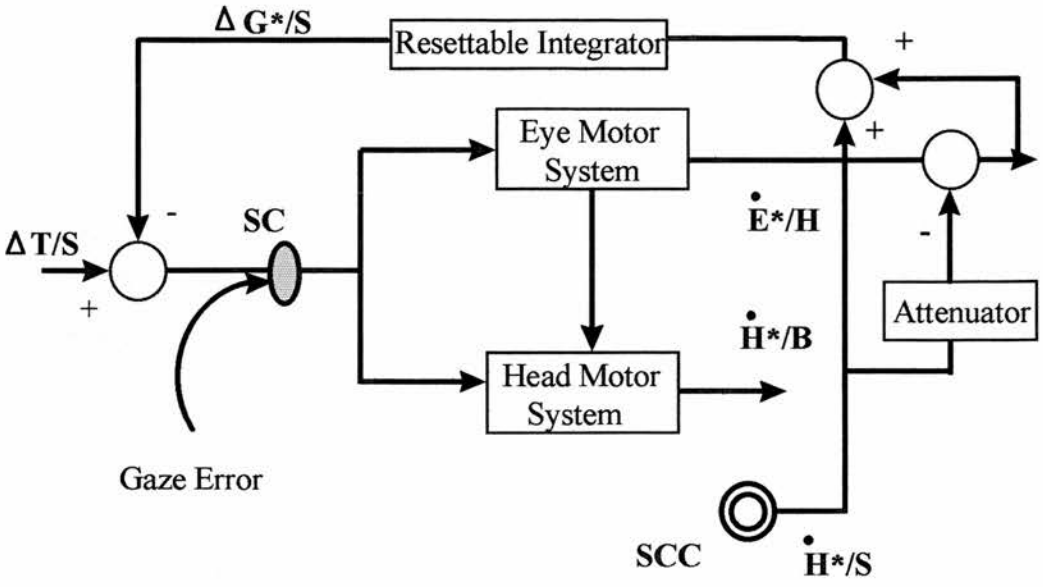



Figure 4.1 Adapted from the gaze control model proposed by Galiana and Guitton (1992). The input to this system is a change in target position relative to space (△T/S). A gaze error signal is then constructed by subtracting gaze relative to space (△G*/S) from the △T/S signal. This forms the input to the superior colliculus (SC) that drives the head and eye motor systems. A corollary discharge (△G*/S) is obtained by integrating the sum of the eye velocity relative to the head ($\dot{E}$*/H) and the head velocity relative to space ($\dot{H}$*/S). The latter signal is assumed to emanate form the semi-circular canals (SCC).

The hypothesis of the experiment described in this chapter is that the superior colliculus does have access to visual information about target location during the burst generation. This hypothesis is based on the primate research discussed in Chapter 2 (page 43) which showed that the sudden appearance of a visual target just prior to movement onset causes a change in the acceleration of the gaze to occur during the movement. This has been linked to a visual target

appearing in the receptive field of the TR(S)N (Munoz and Guitton, 1986, 1989, 1991a, 1991b), and compared to the long transmission delays from the retina to the cortex, the latency of this response is very short (approximately 50 ms, with acceleration changes occurring 20 ms later). The existence of fast conducting retinal axons that project monosynaptically to the TR(S)Ns (Berson and McIlwaine, 1982; Beckstead and Frankfurter, 1983), suggests that a sensory induced activity in these neurons produces a direct motor command for gaze. In cats fast pathways relating to visually driven switching actions have also been described (Pettersson and Lundberg, 1997). If a similar 'fast route' exists in humans, this could provide the superior colliculus with information about changes in target position during the movement, given that the duration of the movement is long enough.

The τ-coupling theory predicts that this visual information could be used to control the gaze approach, and it proposes that instead of position and velocity information the brain perceives and uses τ information. If a subject is asked to make a large gaze shift so that they can pursue a moving object, the theory would predict that the reduction of the gaze-target angle would be achieved by a coupling between a movement τ and a τ-guide. If this is so then it would seem reasonable to suggest that the τ-coupling theory is an attractive alternative to the current models of oculomotor control. Therefore, the second hypothesis of the experiment described below is that the control of gaze shifts can be explained in terms of a coupling between an intrinsically generated τ-guide ($\tau_{guide}$) and a movement τ for the closure of the gaze target gap ($\tau_{GT}$).

In order to test these two hypotheses, subjects were asked to make large gaze shifts to a moving target. This task required them to attend to the motion of the target. In theory they would use an intrinsic τ-guide to guide their approach. Such a task would be familiar to athletes who regularly participate in team sports, such as hockey or football, since during the course of a game they are frequently required to turn their gaze quickly over large angles so that they can to track the motion of the ball or another player.

## 4.2 Method

### 4.2.1 Subjects

Data were collected from a total of nineteen subjects. Following an initial analysis in which the trials were calibrated, six subjects showed a very high degree of oculomotor control so their data was used in further analyses. This group of six subjects was composed of three females and three males and their mean age was 24.6 years. Only one of these subjects had previously participated in eye movement studies, the rest were naive. One subject wore contact lenses to correct for myopia. Data from the other thirteen subjects were not included.

### 4.2.2 Apparatus

Figure 4.2 shows an overhead view of the experiment. Subjects were requested to make large gaze shifts to a small target that was mounted on a motorised linear track (86 cm long). The target consisted of a small black geometric shape placed in the centre of a small red rectangular card (1cm wide by 2cm high). This was mounted onto a metal carriage which could be moved along the track, the

motion being controlled by a BBC Master computer. Subjects were seated so that when they faced forward they were parallel to the track at a distance of 140 cm. This meant that the target subtended approximately 0.4 degrees.

A Selspot$^{TM}$ movement registration system was used to record head and target movements, with one camera being mounted above the subject to monitor motions in yaw, and the other so that its optical axes was vertical and the x axis of its image plane was parallel to the track. The two cameras had overlapping fields of view, and the cameras were calibrated to account for differences in height and focal length (see Appendix II).

The subject's eye movements were recorded using electro-oculography (eog). Four millimetre silver-silver chloride sensors housed in an epoxy ring (supplied by In Vivo Metric, California, USA) were used to maximise stability and reproducibility. The signal was pre-amplified, captured and synchronised via an analogue input to the Selspot system. All data were sampled at 312 Hz.

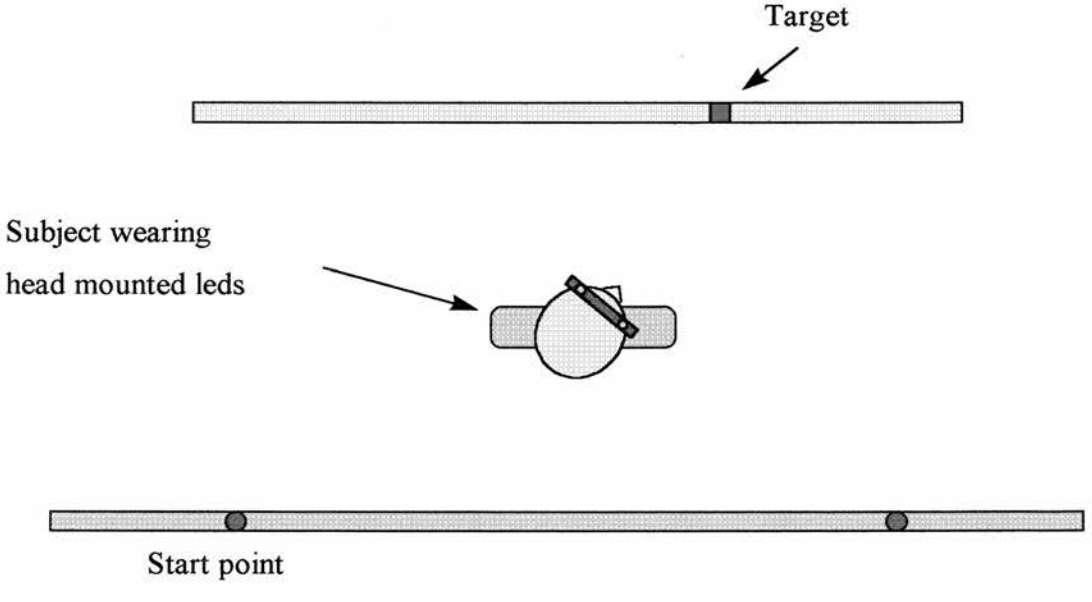



Figure 4.2 Diagram showing an overhead view of the experimental set up.

4.2.3 Procedure

The skin around the subjects' eye was cleaned and abraded using cotton wool and surgical spirit. The electrode cavity was filled with electrode gel and the electrodes were attached to the subjects' outer canthi using adhesive washers. This was done approximately twenty minutes prior to the start of the experiment to allow the signal to stabilise. The subject was also required to wear a headband which had a small cylindrical foam pad attached to the front. Two IRLeds were mounted onto this foam pad, one above each eye. These IRLeds were visible to the camera mounted over the subject's head.

Subjects were seated perpendicular to the linear track so that the target was at eye height. Their task was, on the command "go", to make large horizontal gaze shifts from an initial fixation point to the target. The initial fixation points were situated on a board behind and to the side of the subject, and they were placed so that the subject could see them by maximally turning their head and eyes. Once they had visually grasped the target the subject had to count the number of sides of the geometric shape. They were asked to maintain fixation while doing this. During the experiment the subjects wore headphones through which white noise was played. This was done to eliminate the noise made by the motor on the linear track. The amplitude of the gaze shifts recorded ranged from 107-141 degrees, and the experiment was designed so that when the subject fixated the start point they could not see the target.

Each subject completed a total of sixty-four trials, sixteen in each of the following four experimental conditions:

***(i) Known Static.*** The subject was shown the target location and told that the target would not move. They were asked to remember the target position and make a large gaze shift to the target. This was the only condition in which the subject had prior knowledge of the target's location and motion.

***(ii) Unknown Static.*** Subjects had to make a gaze shift to a static target that was in an unknown position. They did not know whether the target would be moving or stationary.

***(iii) Chasing the target.*** In this condition the target was moving at a constant velocity in the same direction as the subject's gaze shift so they had to chase it in order to catch it. They were not told whether the target would be moving or stationary.

***(iv) Meeting the target***. Here the target was moving with a constant velocity in the opposite direction to the gaze shift so that the subject's gaze met the target. Again, the subjects were not told whether or not the target would be moving.

Trials were randomised, and each condition had equal numbers of leftwards and rightwards gaze shifts. In conditions (iii) and (iv) where the target was moving, the target velocity was constant but was varied from trial to trial in the range of 0.15-0.3 m/s.

### 4.2.4 Electro-Oculography Calibration

The eog signal was calibrated at the end of each trial. This was done by asking the subject to fixate the target and rotate their head in yaw so that a full range of eye movements were recorded. The gain and offset of the eog signal were estimated by calculating a linear regression coefficient, r (using the least square

method), for the head to target angle plotted against the eog signal. Trials where there was considerable variance in the signals, that is the $r^2$ value was less than 0.95, were repeated. Trials where drift occurred were also repeated. Drift was defined as a change in the gaze target angle of more than three degrees, during the fixation period at the end of the trial.

### 4.2.5 Gaze Target Angle

This is depicted in Figure 4.3 and was defined as the angle between the line of sight (CG) and the line between the mid point between the eyes and the target (CT). It was the angular gap between the subjects gaze and the target at any point in time. It was computed by summing the instantaneous angle between the head and the target and the angle of the eye within the head.

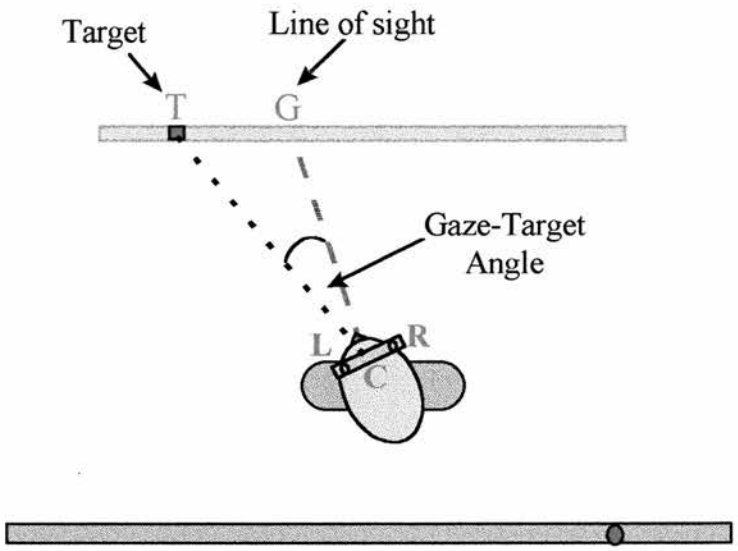



Figure 4.3 Diagram showing the gaze-target angle

4.2.6 Gaze World Angle

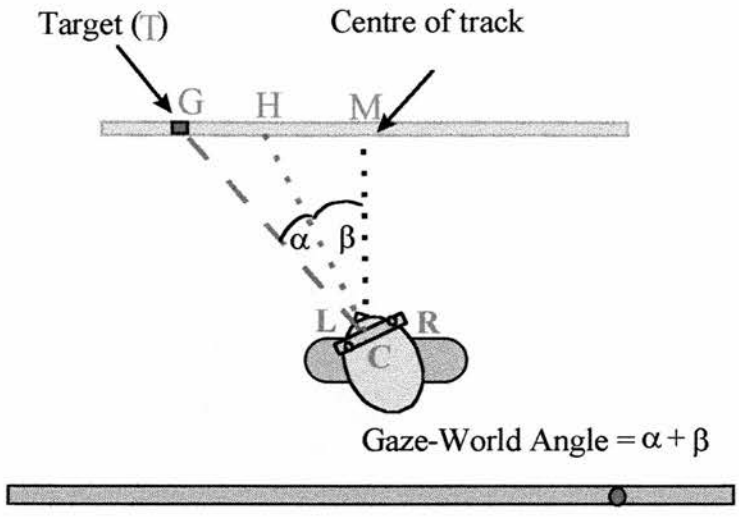



Figure 4.4 Diagram showing the gaze-world angle

As shown in Figure 4.4, the gaze world angle corresponded to the angle between the line of sight (CG) and a fixed point in the environment; the centre of the track (CM). It represented the movement of the subject relative to a fixed place so changes to this angle were caused solely by the subjects' movement and not the motion of the target. It was computed by summing the instantaneous angle between the head and the centre point of the track (HCM) and the angle of the eye within the head (TCH). Velocity profiles were obtained for both the gaze-target and gaze-world angles using finite differences.

4.2.7 Initial Angular Error

This was a measure of the subjects' accuracy. It was defined as the angle between the target and the line of sight (the gaze-target angle) when the velocity of

the gaze-world angle first became zero, that is when the subjects' gaze first stopped in space. This was measured as β-α, as shown in Figure 4.5.

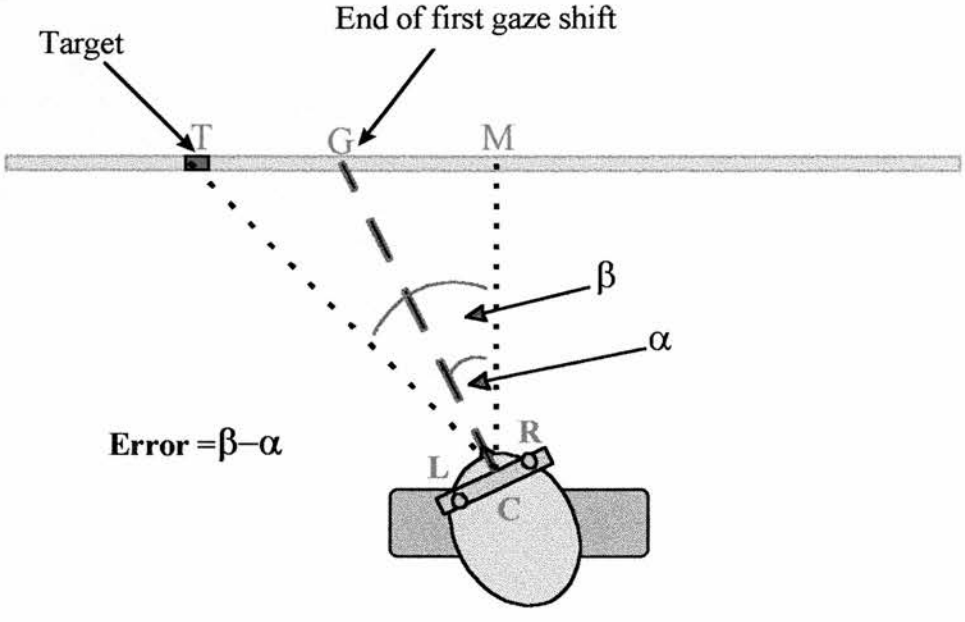



Figure 4.5 Diagram showing the angular error measurements made at the end of the subject's primary gaze movement.

4.2.8 Range of target locations

In order to assess the range of target locations used for each subject the gaze-world angle at a time when the head (line LCR) was parallel to the track (line TM) and the eye fixated the target was calculated for each trial. This always occurred during the calibration procedure. The range of locations was then determined by summing the maximum and minimum angles.

## 4.3 Results

### 4.3.1 Were the gaze shifts prospectively controlled?

In order to answer this an assessment of the level of accuracy and evidence for on-line control was made.

### 4.3.2 Accuracy

Figure 4.6 and Appendix III shows that the subjects were consistently accurate in all conditions. Mean angular errors at the end of the primary gaze saccade were less than $5^0$ throughout (Figure 4.6a). Since the mean range of target locations was $34^0$ (s.d.=4.8) the subjects' level of accuracy was considerably greater than would be expected had they been guessing the target's location. In order to achieve this level of accuracy the subjects must have been using visual information to guide their movements on-line since in some of the conditions no other source of information was available to them. In particular a high degree of precision was shown in the chasing and meeting conditions (RMS errors of 3.168 and 4.24 respectively) where the use of visual information during the course of the movement would have been essential for accurate control. Had the subjects been using the kind of control strategy outlined in the Galiana and Guitton (1992) model (Figure 4.1) they would have initially guessed the target's location and subsequently made corrective movements based on an assessment of the gaze error at the end of the first saccade. Such a strategy could have resulted in low mean errors (due to the combined effects of overshooting and undershooting the target), but considerable variation about the mean would be expected. The low standard deviations shown by all subjects in all conditions (Figure 4.6b) showed that this was not the case for these

subjects. The maximum error that a subject could have made was in excess of $34^0$, yet the greatest mean standard deviation shown by any subject was less than $10^0$, and this was for subject one in the meeting condition. Further support for a highly consistent level of control was provided by low RMS errors (Table 4.1). These data are inconsistent with the Galiana-Guitton (1992) model.

(a) Mean Angular Errors (b) Standard Deviations

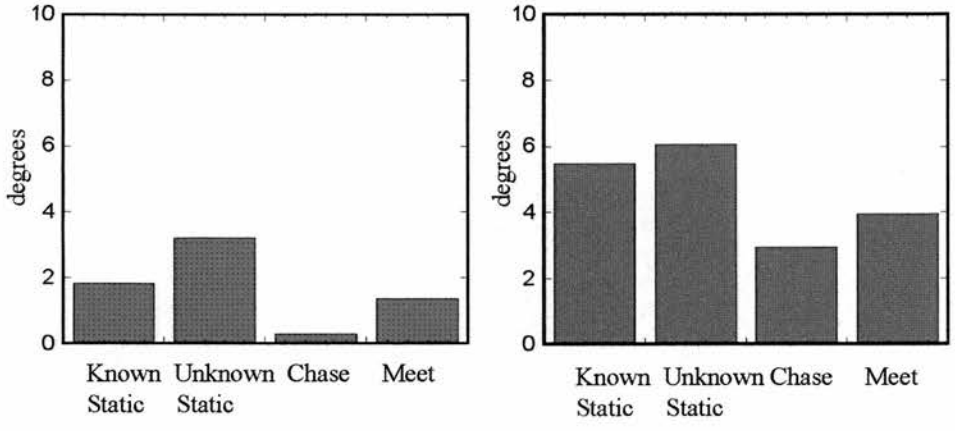



Figure 4.6 Mean data for all six subjects is shown for (a) the mean angular error across all trials and (b) the standard deviation.

| | Mean Error (deg) | S.D. (deg) | RMS Error (deg) |
|---|---|---|---|
| Known Stationary Target | 3.216 | 6.059 | 7.037 |
| Unknown Stationary Target | 1.841 | 5.478 | 5.593 |
| Chasing The Target | 0.310 | 2.929 | 3.168 |
| Meeting The Target | 1.376 | 3.948 | 4.242 |

Table 4.1 Means for all subjects for mean error, standard deviation and RMS error in all conditions.

4.3.3 Evidence for on-line adjustment

The high level of accuracy shown by the subjects indicated that they were adjusting their gaze trajectories at some point during the movement. To try and determine how they were being adjusted, gaze-world velocity profiles for all subjects were examined. Typically, as shown in Figure 4.7, the gaze-world velocity profiles for the known target condition were smooth and bell shaped. In the other conditions the profiles were not so smooth and showed a considerable amount of variation. Indeed, some of the profiles were positively skewed.

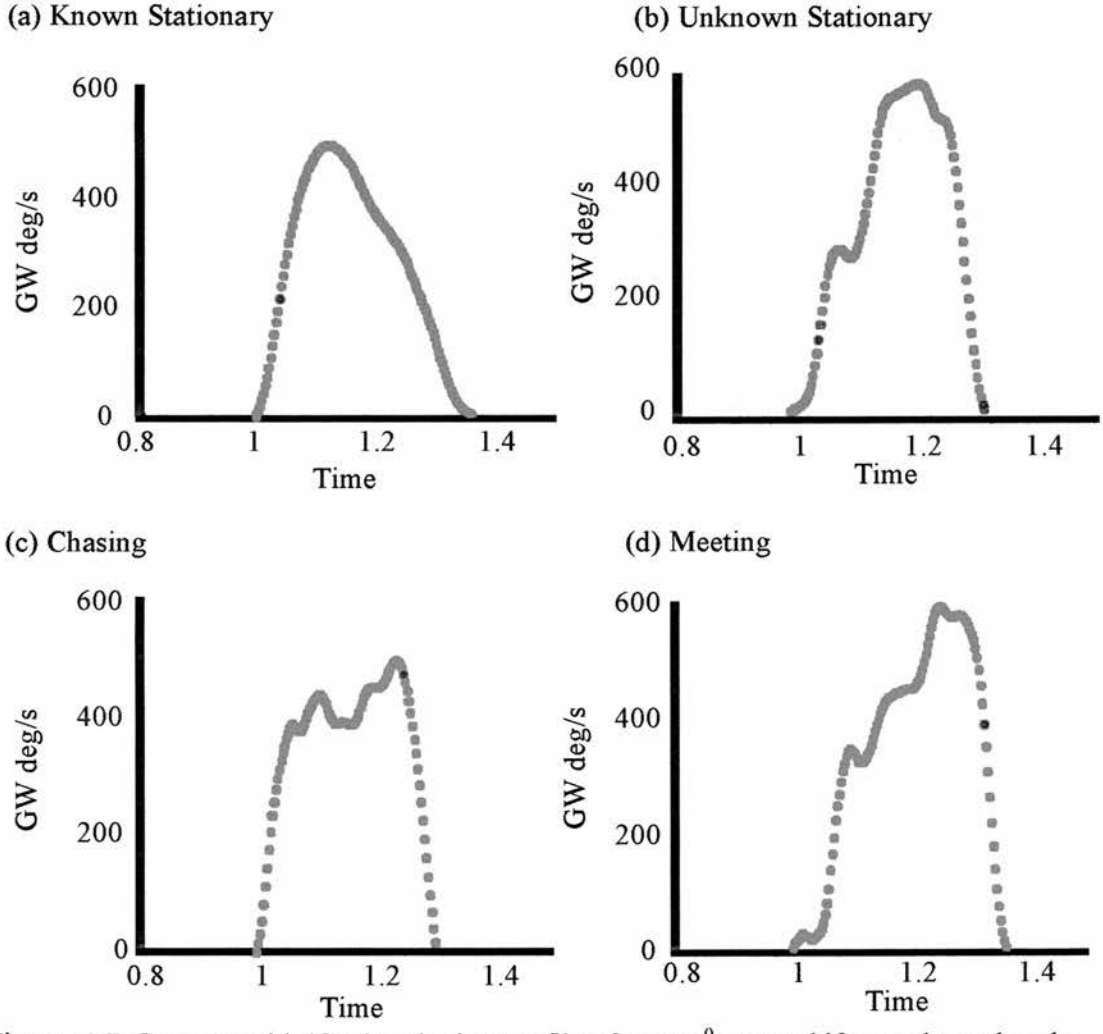



Figure 4.7 Gaze World (GW) velocity profiles for $140^0$ gaze shifts made under the four different conditions by S3.

4.3.4 The degree of τ-coupling between a τ-guide and a movement τ.

The τ-coupling theory would predict that these gaze shifts would be controlled by a coupling a τ-guide and a the gaze-target movement τ. If such a relationship exists then plotting these τs against one another should result in a straight line. If the coupling is strong then the $r^2$ value (the proportion of variation in the data that is accounted for by the linear regression) should be close to one for a considerable percentage of the movement time. The sample plots in Figure 4.8 show that when all the data are taken into account a strong coupling exists between an intrinsic τ-guide ($\tau_{guide}$) and a movement τ ($\tau_{GT}$) for the known stationary condition, but not for the other conditions. This suggests that τ-coupling is a weak predictor of behaviour in the conditions where the target's location and motion were initially unknown. This may be because in these movements an estimate of the guide's duration (T), the parameter needed to generate the guide, was not available. This implies that in order to generate a τ-coupling that would be useful in guiding the gaze shift in these conditions, visual information about the target was a prerequisite. The level of accuracy shown by the subjects suggests that useful visual information was available during the gaze shift, but not from the movement onset. Thus, had the plots for these conditions (conditions b to d in Figure 4.8) been straight then the τ-coupling theory would have had to be rejected since it would not have been possible to create an effective τ-guide.

The extent and duration of τ-couplings were assessed using the linear regression procedure and the Bland Altman method of agreement outlined in Chapter 3. The start of coupling, as described in Chapter 3 corresponded to the first

data point in the series where the relative deviation was less than two and the $r^2$ value was in excess of 0.96.

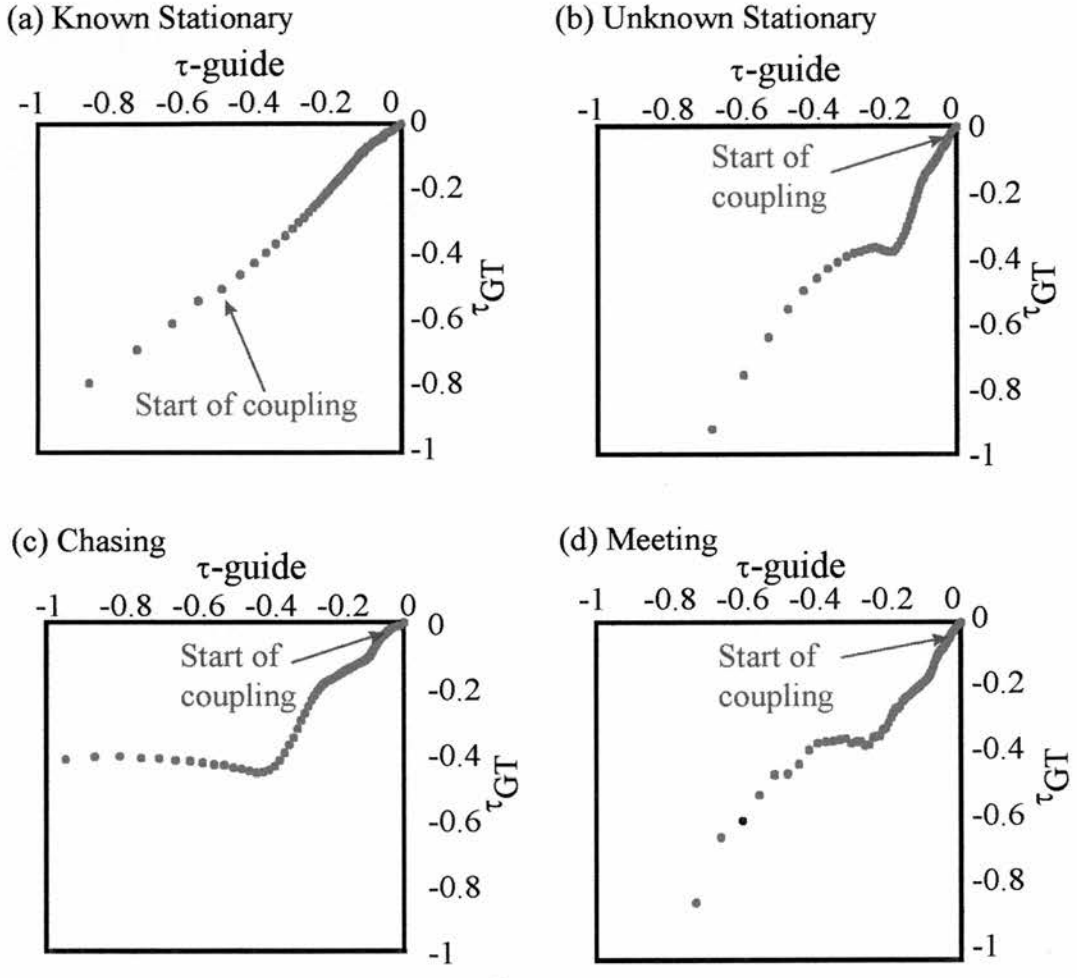



Figure 4.8 τ-coupling plots for $140^0$ gaze shifts made under the four different conditions by S3.

Initially this analysis was run on all the data, and as Figure 4.8 and the data in Appendix III demonstrate the duration of coupling varied considerably with respect to condition. When the subject knew where the target was (Figure 4.8a) the coupling started much earlier in the movement than in the conditions where the target's location was unknown prior to movement onset. Figure 4.9 shows the percentage of

movement time for which τ-coupling existed for the different conditions, and a one-way ANOVA confirmed that there were large significant difference between the four conditions ($F_{(3,15)}$=2061 $p<0.001$). Post hoc Tukey HSD test indicated that the known static condition, with a mean of 90.34%, was significantly greater than the other conditions where τ-coupling lasted for approximately the last 15% of the movement time. This corresponded to a duration of approximately 50ms (unknown static $\bar{x}$ =45.63 sd=12.34, chase $\bar{x}$ =46.65 sd=21.49, meet $\bar{x}$ =53.29 sd=22.87).

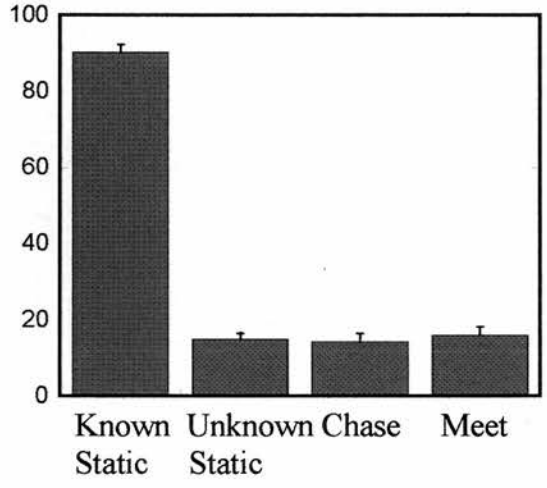



Figure 4.9 Mean and standard deviation of the percentage of total movement time when τ-coupling existed for each of the four conditions.

Since in those conditions which necessitated on-line control it was possible that a τ-guide had been initiated during the movement it seemed logical to assess the extent of τ-coupling when the start time of the τ-guide was adjusted. This was done by calculating a series of τ-guides for each trial, and these corresponded to start points at every 3.125ms during the movement. There were no instances when this procedure increased the duration or the $r^2$ values for τ-coupling.

4.3.3 Target information prior to τ-coupling onset.

If the subjects were using a τ-coupling strategy then they must have had sufficient access to target information to create an effective τ-guide. In the known static condition this information was available to them from the memory, in the other conditions it would have had to have been gained visually. Due to the oculo-motor delay it seems reasonable to suggest that information about the target was gained at least 100ms prior to the start of τ-coupling. If the target was beyond the field of vision at this point then the τ-coupling hypothesis would not be a valid explanation of their behaviour. Figure 4.10 shows that, in the conditions where the τ-guide was initiated during the movement, the gaze-target gap was less, on average, than $60^0$ which is well within the visual field. However, the mean velocity of the gap closure was in excess of $450^0$/sec.

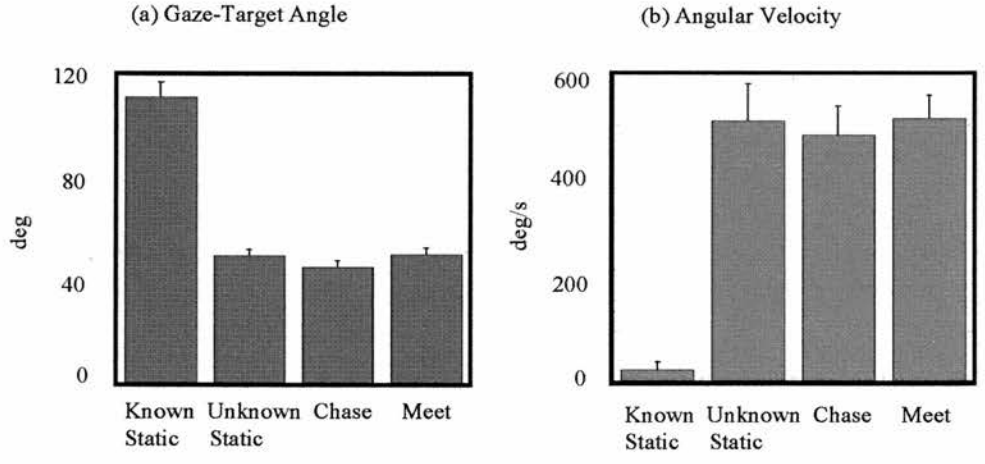



Figure 4.10 Mean and standard deviations of the subject's means for all conditions for (a) gaze-target angle and (b) gaze-target velocity at 100ms prior to the onset of coupling.

4.4 Discussion

This experiment showed that some subjects were able to prospectively control their gaze movements using on-line visual information. This control could be described in terms of the coupling of a movement $\tau$ ($\tau_{GT}$) onto a constant acceleration intrinsic $\tau$-guide, however, the duration of any such $\tau$-coupling was dependent upon information about the target being available. Thus, the ability to demonstrate behaviour which is compatible with the accurate and efficient use of an intrinsic $\tau$-guide is dependent upon being able to predict, with great precision, the required duration of $\tau$-guide. This ability varied between individuals, indeed it was interesting to note that only six out of the nineteen subjects were able to exhibit this degree of oculomotor control, and that these six were all very competent ball sports players.

These results suggest that for the $\tau$-guide to be a plausible control mechanism the initiation of a $\tau$-guide, and the onset of $\tau$-coupling, must be able to occur during a movement as well as prior to movement onset. This implies that when the gap is initially unknown a predictive estimate is used to guide the action, but when expropriospecific information becomes available there is a switching between the predictive and prospective forms of guidance. In the case of the gaze shifts in this experiment where the target location was unknown this switching would have occurred so that prospective $\tau$-coupling existed for approximately 50 msecs. Although this appears to be a relatively short duration for $\tau$-coupling this time course is similar to that found be Lefèvre et al. (1992). They studied the modulation of the vestibulo-ocular reflex (VOR) in humans making large gaze shifts and demonstrated

that the VOR is inhibited during a gaze shift but this then restored approximately 40 msec prior to the end of the movement. They suggested that this could be related to the firing of the omnipause neurons (OPNs) since, in cats, OPNs have been found to stop firing prior to movement onset and resume firing just prior to the end of the movement (Paré and Guitton, 1991). Lefèvre et al. concluded that their subjects were able to foresee a constant duration towards the end of the gaze shift during which they 'switched on' their VOR.

Evidence for large gaze shifts being prospectively controlled is in accord with the data of Zee et al (1976) who found that the control of long duration movements could be adapted on-line. Unlike Zee et al.'s patients though, the subjects in this present experiment were healthy and were able to make gaze shifts that were in excess of 500 deg/sec. This suggests that the high velocity of the gap closure, and the subsequent blurring of the visual image, was not a limiting factor in the control of these movements. Since the red target was the only moving object in the environment, its motion against the optic flow field created by the subject's own movement could have provided a sharp discontinuity that was particularly informative. The small value of $\tau_{GT}$ when this information became available (approximately 150ms), was suggestive of this information provoking the initiation of a very fast response. If, like primates, humans also have very fast retinal projections to the superior colliculi then this could provide a possible neural mechanism for this behaviour.

In order to account for these results the $\tau$-guide hypothesis cannot simply be seen as a feedforward mechanism since the $\tau$-coupling appears to be intermittent.

However, since under certain conditions the gaze shifts did not appear to be ballistic these data also contradict the systems models that have attempted to model gaze shifts (for example, Galiana and Guitton, 1992, and Phillips et al., 1995). By relying on a local internal feedback loop these models have no means of allowing for the possibility of on-line prospective control utilising visual information. Future models for the superior colliculus and brain stem circuitry need to incorporate feedback as well as feedforward mechanisms. That is, they need to account for the use of expropriospecific and proprioceptive information and not solely exteroceptive information.

Finally, this investigation questions the level at which a τ-coupling control mechanism might operate. The close relationship that has been reported between the pulse of activity in the agonist muscles and short lead burst neurons in the brain stem would indicate that at this level neuronal firing rates 'code' for velocity, and burst duration relates to the movement amplitude (Henn and Cohen, 1976, Hepp and Henn, 1979, Keller, 1974, van Gisbergen et al., 1981). This would suggest that either movement τs are 'higher order' commands, or that they simply emerge as a consequence of some other kind of control mechanism. If the former explanation is assumed to be true then it becomes necessary to predict possible mechanisms which could account for τ-coupling.

One such model which describes how τ-coupling might be involved in orienting gaze shifts that involve the superior colliculus is outlined in Figure 4.11. This model proposes that prior to movement onset the sensory information entering the superficial areas of the superior colliculus relates to a guiding τ for the gaze-target gap. This may be predictive, remembered or perceptual in nature and is

expressed as a level of neuronal activity at a particular location on this telotopic map. This activity is then 'translated' into changes in the locus of activity on motor map in the deep layers of superior colliculus, and in particular the activity of oTRSNs and fTRSNs. The changing levels of activity at specific places on these maps contributes to the motor command that is sent to the brain stem burst generator where a movement $\tau$ emerges. The ensuing changes in gaze alters the $\tau$ of the gaze-target gap and this creates a changing pattern in sensory flow fields. These give rise to a perceptual $\tau$ of the physical gap, and it is this perceptual $\tau$ that is coupled to the $\tau$-guide.

Within this model there are various types of $\tau$ like information and the coupling between them is distributed. First, there is a coupling between sensory $\tau$s and intentional $\tau$-guides which gives rise to a predictive estimate for the movement. This process is likely involve the parietal and frontal cortices and is, therefore, unlikely to form a direct perception-action coupling. However, a more direct coupling between a perceptual $\tau$ from retinal information and the movement $\tau$ is proposed at the level of superior colliculus, and it is speculated that this is mediated via fast retinal projections. Finally, it is also suggested that $\tau$-coupling occurs at the level of the cerebellum where retinal and extra-retinal information is monitored and co-ordinated with movement information. The cerebellum plays a pivotal role in this model, and this will be discussed in greater detail in Chapter 5.

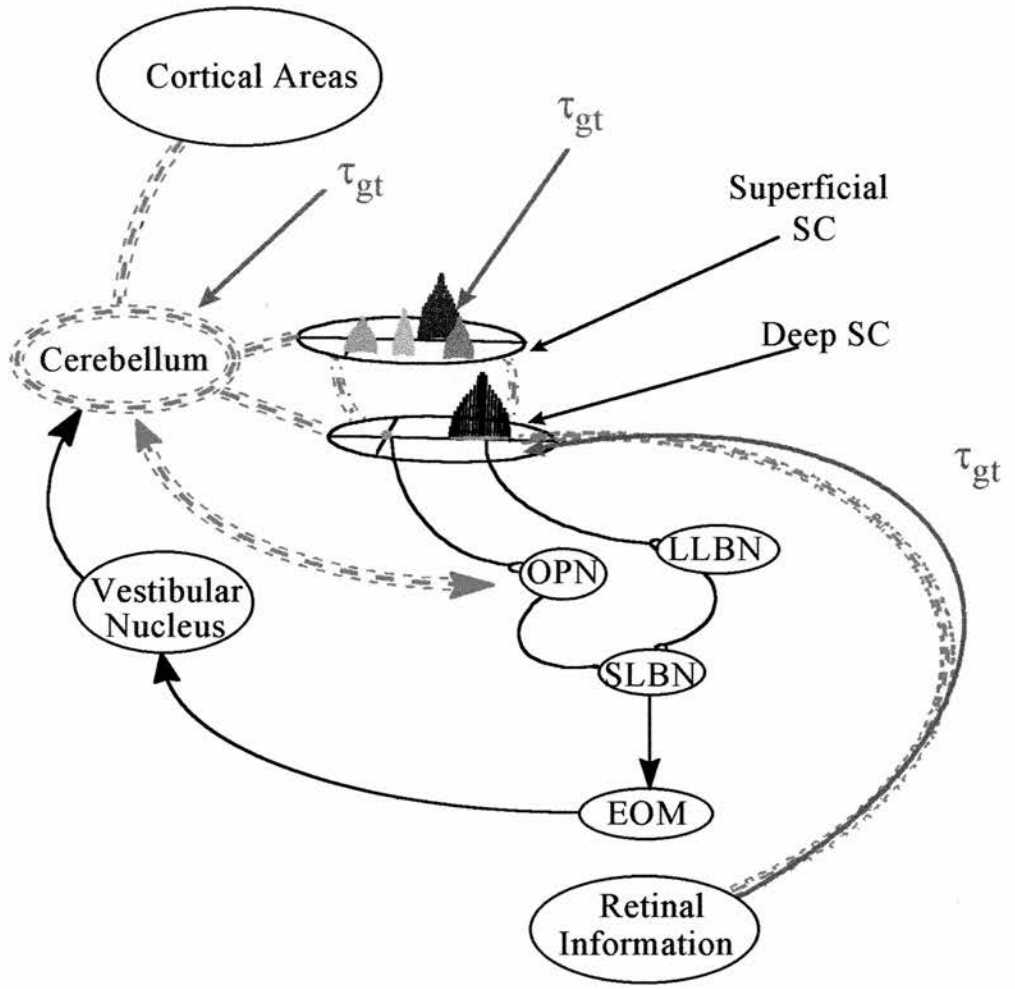



Figure 4.11 A τ-coupling model for gaze control. Couplings are indicated by bold spotted red lines. Perceptual or guiding τs are shown in green.

The schematic model shown in Figure 4.12 extends the original model proposed by Lee et al. (1998b) by incorporating sensory information that is not in a τ format. While this is not necessarily a problem for the τ theory it does question the extent to which Gibson's ideas on direct perception can be seen as viable. An 'indirect' model of the τ-coupling is necessary to account for the populations of neurons that carry position, velocity or acceleration signals. For example, the vestibular system provides the CNS with information that is not in τ form, when the

head is turned the firing rate in the vestibular nucleus is proportional to instantaneous head velocity, yet, the results from this study suggest that the gaze-target τ is a control parameter. Thus, the probability that τ is the only form of information neurally represented seems remote. It seems more likely that multiple sensory inputs from a variety of different sources are used to define and monitor the coupling of certain perceptual and motor τs.

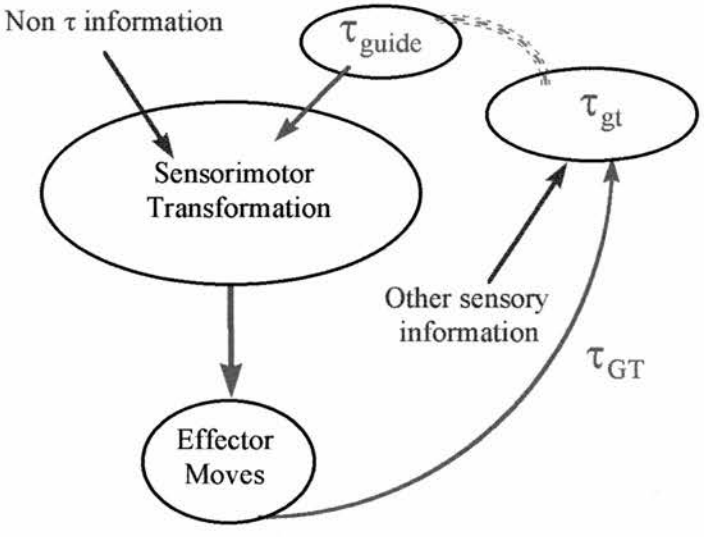



Figure 4.12 An extended general τ-coupling model for the control of an action that utilises an intrinsic τ-guide. τ like information is indicated by blue, non-τ information in green, and coupling in red.

In conclusion, the findings from this experiment provide evidence to support the generalised τ-coupling theory. When the target was in a known stationary position a τ-coupling existed for approximately ninety percent of the movement, whereas in the conditions where the subject's only option would have been to initiate an intrinsic τ-guide during the movement the duration of the τ-coupling was much

shorter (approximately 50ms). Under the conditions which necessitated on-line visual control an estimate of the gaze-target angle 100ms prior to the coupling onset revealed that had the τ-coupling existed for a considerably longer period of time then the subject would not have been able to see the target and initiate a τ-guide. In these conditions a τ-coupling of ninety percent of the movement would not have provided support for the τ-coupling theory since the subject could not have possibly estimated the duration for the τ-guide.

# Chapter 5 : The Cerebellum

## 5.1 Introduction

In 1824 Flourens noted that the cerebellar cortex plays an important part in the regulation of movements, a conclusion that was later to be supported by the pioneering work of Holmes (1917). These early observations indicated that cerebellar damage resulted in the disruption, but not abolition, of movements and this led to a general belief that the cerebellum is a movement regulator as oppose to a movement generator. However, it was not until the work of Eccles et al. (1967) that the functional role of the cerebellum really started to be understood. He demonstrated that the output from the cerebellar cortex was inhibitory, and that it influenced the control of movement by inhibiting or disinihibiting the actions of the brainstem, sensorimotor cortex and spinal cord. Today, a definitive theory for the cerebellum still appears to be some way off, but there are numerous theories which have provided insights into its role and function. These theories can roughly be divided into two categories; those which focus on how the cerebellum operates, and those which address the functions in which it participates. The $\tau$-coupling theory is concerned with both of these aspects since it makes predictions about how an organism behaves in an environment and theorises about the nature of central control mechanisms. Thus, the $\tau$-coupling theory could play an important role in furthering our understanding of how the cerebellum functions. Conversely, if the cerebellum is shown to operate in a manner that cannot be accounted for by the $\tau$-coupling theory, then the validity of this theory must be questioned.

The aims of this chapter are threefold. The first is to discuss various models and theories of cerebellar function in relation to the τ-coupling theory. The second is to make predictions as to how τ-coupling would be affected by cerebellar damage, and the third is to assess those predictions by examining the nature of τ-coupling in the control of volitional movements in a human who has cerebellar damage.

## 5.2 Models and Theories of the Cerebellum

It has been suggested that the cerebellum acts as a mediator, a predictor, a pattern generator and a sensory mechanism, and it is also thought to play an important role in motor learning. If the τ-coupling theory is going to provide a viable addition to these established theories and ideas then the data that have given rise to them should be compatible with the ideas of Lee et al. (1998b). It should also be possible to make predictions about how cerebellar damage will alter τ-couplings.

### 5.2.1 The cerebellum and motor learning

Perhaps one of the most controversial areas of cerebellum function concerns its role in motor learning. Motor learning involves adjusting the magnitude and timing of muscle contractions so that the effector limb produces an appropriate force which is applied in the right direction at the right time. Marr's (1969) theory of cerebellar learning, which was subsequently refined by Albus (1971), has been highly influential in this field and much of its appeal lies in the fact that it elegantly links psychology and physiology. The anatomy of the cerebellum is unique. Its cortex has two types of afferent input; mossy fibres and climbing fibres. Output signals from cerebellum come from the cerebellar nuclei via Purkinje cells.

Mossy fibre inputs to the cerebellar cortex synapse onto the dendrites of granular cells. Axons from these granular cells ascend and branch to form parallel fibres which synapse onto the dendrites of numerous Purkinje cells. Climbing fibres on the other hand ascend through the granular cells where each fibre synapses onto just one Purkinje cell. The basic premise of the Marr-Albus theory is that if the mossy fibre activation of a Purkinje cell (via parallel fibres) is coincident with the climbing fibre activation on the same Purkinje cell, then a modification to the synapse between the parallel fibre and Purkinje cell will occur. Eventually the changes in synaptic function are such that mossy fibre input alone will produce a particular pattern of Purkinje cell activation. That is, the climbing fibre acts as a sort of teacher by wiping out inappropriately strong synapses between the parallel fibres and Purkinje cells, so that the Purkinje cell 'learns' to respond to a particular subset of parallel fibre inputs. The activation of Purkinje cells has an inhibitory effect on the cerebellar nuclei, so the patterns of activation in the parallel fibre contribute to the co-ordination of a movement.

Notwithstanding this elegant theory, the question of whether or not the cerebellum is involved in conditioning is still open to debate. While scientists such as Glickstein and Yeo (Yeo and Hardiman, 1988, Glickstein and Yeo, 1990) strongly believe that it is, others such as Bloedel and colleagues are less convinced, since they have shown that the nictitating membrane response of the rabbit, which has been used in demonstrations of cerebellar learning, can be re-acquired after the cerebellum has been completely removed (Kelly et al., 1990). However, the literature tends to favour the suggestion that having an intact cerebellum will enhance the chances of learning. If this is the case then in terms of $\tau$-coupling theory cerebellar damage

could lead to two possible deficits. First, we might suppose that the cerebellar patient would show an inability to refine the estimated duration of an intrinsic τ guide when learning a new task, and this would result in hypometric or hypermetric movements. Second, the patient might be deficient in their ability to establish new patterns of simultaneous or sequential τ-couplings.

5.2.2 The cerebellum as an adjustable pattern generator.

One popular idea about the cerebellum is that it functions as an adjustable pattern generator and there is some common ground between this notion and that of τ-coupling. Blomfield and Marr (1970) suggested that prior to movement onset a large set of neurons fire in the motor cortex. This pattern of activity is in excess of that required for the action and inhibitory Purkinje cell activity eliminates the unnecessary commands via the pathways that link the cerebellar nuclei and the motor cortex. This idea, that movements are generated as a result of feedback through a recurrent network, was reinforced by Houk and Krubert (1988) who proposed a model known as the Adjustable Pattern Generator (APG). APGs are 'anatomical modules' composed of parallel fibres, climbing fibres, Purkinje cells and a positive feedback loop between a cerebellar nucleus and a motor cortical cell. The cerebellar nucleus cell within an APG receives an inhibitory input from a set of Purkinje cells and silencing this inhibition permits a burst command to occur that has an adjustable intensity and duration. This idea of a burst command is similar to the idea of an intrinsic τ-guide, in that it, too, can be defined prior to movement onset, has a defined duration and a variable intensity of firing.

Houk et al. (1996) proposed that the 'programming' of a movement (e.g. the 'choosing' of the duration and k value for an intrinsic τ-guide) is instigated through mossy fibre input. This instruction signal causes some of the Purkinje cells to switch on and others to switch off, but does not initiate the movement. Movement initiation occurs when a sensory or internal input to the motor cortex switches the network between the motor and cerebellar cortices from being inactive to active. It is this that releases the adjustable pattern generator. Again parallels can be drawn with the τ-coupling theory, or at least the concept of an intrinsic τ-guide. The coupling between the τ-guide and a movement τ could occur within the cerebellar-motor cortex loop, and since the Purkinje cells receive training from climbing fibre inputs, different coupling strategies (values of k) could be set up.

The APG model is essentially open loop and does not allow for on-line prospective control from external stimuli and cannot, therefore, explain any effects of extrinsic coupling. However, in the τ-coupling theory the relative dominance of intrinsic and extrinsic τ-guides is undefined, and it does not specify whether intrinsic τ-guides may, or may not, be used in conjunction with extrinsic τ-guides, or whether the expropriospecific information available during an extrinsic τ-coupling is to be used in isolation or to create an intrinsic τ-guide.

### 5.2.3 The planning and execution of movements.

Different regions of the cerebellum are known to be involved in different activities. For instance, the hemispheres are thought to control the co-ordination of volitional movements, while lesions to the midline result in problems with postural

stability and gait. Functional specialisation has also been noted for the planning and execution of movements. Brooks (1984) determined that the dentate nucleus is important for the planning of future movements while the interpositus nucleus is involved with the control of ongoing movements. This latter relationship was studied by Burton and Onoda (1977) who recorded the firing rates of interpositus nucleus neurons during the flexion and extension of the elbow joint. They found neurons had either maximal or minimal discharge rates at the time of peak angular velocity of the limb, and since group II afferents from muscle spindles have both excitatory and inhibitory actions on interpositus neurons (Kawaguchi and Ohno, 1974), they suggested that this strong correlation between the interpositus firing rates and limb velocity could have been mediated via the spindles.

In terms of the τ-coupling theory these findings would suggest that lesions to the dentate nucleus could result in an inappropriate preparation of intrinsic τ-guide duration, whereas lesions to the interpositus nucleus would be more likely to create difficulties in the co-ordination of τ-coupling in a movement.

### 5.2.4 The cerebellum as a timing device.

The dyskinetic movement patterns of patients with cerebellar disease would suggest that the cerebellum plays an important role in the timing of movements. This has been confirmed by the work of Ivry and Keele (1989) who found that patients with lateral cerebellar lesions had problems judging time intervals (they appeared to have an abnormal 'central timekeeper'), while those with medial lesions had problems making movements at specified times (i.e. they showed an impairment in implementing periodic movements).

Braitenberg (1961) suggested that the unique physiological structure of the cerebellum may result in the generation of patterns of activity at regular intervals. He pointed out that despite the folding of the cerebellar cortex, the molecular layer has a uniform thickness and the parallel fibres are unexpectedly straight. Moreover, the dendrites of the Purkinje cells, which lie perpendicular to the parallel fibres, are arranged so that they stay parallel to each other. He concluded that the cerebellum acts as a timing device in which the parallel fibres act as delay lines and the climbing fibres as a clock read out. He proposed that coincident climbing and parallel fibre volleys would ensure that afferent signals moving across the cerebellar cortex were 'transformed' into appropriately timed and sequenced Purkinje cell activity. However, Stein and Glickstein (1992) suggested that the duration of most movements is considerably longer than the time it takes for a volley to travel the length of a parallel fibre, if this is the case then it makes it difficult for this theory to account for their control. It is still unclear how a τ-coupling might relate to this theory since the representation of perceptual, sensory or movement τs in terms of patterns of spreading Purkinje cell activity is not known. However, it is possible that the structure of the cerebellum could provide a mechanism by which different τs could be coupled, and this would imply that damage to the cerebellum would result in a deficit in the co-ordination of τ-couplings.

### 5.2.5 Is the cerebellum a mediator, comparator or predictor?

Support for the notion that the cerebellum is critically involved in the co-ordination of simultaneous tasks came from Vercher and Gauthier (1988) who investigated the role of dentate lesions on oculomotor tracking performance in

baboons. They showed that lesions had little effect on eye tracking alone, but performance decrements were prominent when the baboons tracked with both their eyes and their hand. This suggests that the cerebellum is involved in comparing and co-ordinating sensory inputs and output, and tasks which involve visual guidance are likely to be compromised following cerebellar damage since they require the integration of exterospecific, propriospecific and expropriospecific information which needs to be used both predictively and prospectively. Beppu et al. (1987) reinforced this by demonstrating improvements in manual pursuit in cerebellar patients when vision was removed. Since the cerebellum appears to be specifically concerned with the use of visual information in the co-ordination of the trunk and limbs for movement and posture, possible $\tau$-coupling deficits would be those that involve visuomotor control and actions that involve the integration and co-ordination of visual and non-visual information.

A further hypothesis for cerebellar function was forwarded by Bloedel (1994) who proposed the Vermittler hypothesis. This suggests that the cerebellum integrates properties of external space with other movement related information and operates as an on-line mediator whose output provides the central nervous system with an integrated signal that relates external and internal information. This too implies that cerebellar damage will produce performance decrements in complex tasks with multiple perceptual and motor couplings.

The notion that the cerebellum's role is that of a comparator which evaluates desired positions, velocities, accelerations with actual values, has been popular to account for feedback processes in movement control, while theories which suggest that it functions as a parameter calibrator or predictor (such as the Smith Predictor

theory by Miall et al., 1993) have tried account for feedforward processes. These theories would lead to the prediction that cerebellar patients would have problems in both establishing an intrinsic τ-guide and in τ-coupling. However, the idea that the cerebellum is involved in prediction has been challenged in a study by Waterston, Barnes and Grealy (1992), who demonstrated that the predictive mechanisms involved in pursuit eye movements are spared in patients with cerebellar disease. In terms of τ-coupling, Waterston et al.'s finding suggests that cerebellar patients would not be deficient in choosing an appropriate intrinsic τ-guides, but they would be less able to τ-couple and execute an appropriate movement.

5.2.6 The cerebellum as a sensory mechanism

The notion that the cerebellum is a sensory mechanism was proposed by Bower (1996) who noted that many sensory systems project to the cerebellum and that its outputs are equally diverse. Consequently, he has suggested that the cerebellum's role is primarily that of a sensory co-ordinator and its function is to acquire high quality sensory information which it then makes available to the rest of the central nervous system. Rather than being involved in either perception or motor co-ordination the cerebellum's purpose is to assure good data for both, and damage will result in the manifestation of performance decrements on complex tasks that involve co-ordinating sensory information from multiple sources. It follows that if the cerebellum is unable to acquire adequate perceptual information, it will indirectly affect the efficiency of other systems. This theory implies that during limb movements the cerebellum would monitor sensory information and influence the gamma efference so as to provide a gain control mechanism for the muscle spindles.

If this view of the cerebellum is correct then the inappropriate following of, or the generation of an inappropriate intrinsic τ-guide would be a predicted deficit of cerebellar damage. This theory would also predict that simple τ-couplings would be less affected than complex τ-couplings.

5.2.7 The cerebellum, mental imagery and the internal representation of timing

τ theory requires that in order to use an intrinsic τ-guide the duration of a movement must be predicted. This implies that the future movement time must be neurally represented prior to the movement onset. Decety and Michel (1989) showed that in healthy adults performing tasks such as writing that this was the case. They demonstrated that there is little variation in the time taken to perform an action either overtly or mentally. However, a further experiment by Decety et al. (1989) indicated that the force required to achieve an action was an important parameter used to plan movements. They asked blindfolded subjects to either physically or mentally imagine walking to targets with and without a heavy rucksack. They observed a significant increase in the duration of the mental walking condition with a load, and concluded that in the overt loaded condition subjects had programmed an increase in force so that they could overcome the resistance and maintain the standard walking speed, whereas in the mental condition an increase encoding of force was not applied so mental walking speed was slower and the estimated duration was increased. This result suggests that our prediction of movement duration is not always accurate, and would imply that intrinsic τ-guides may not always be accurately defined prior to movement onset. This implies one of three

things; either the idea of an intrinsic τ-guide is incorrect, or mental and physical movements use different temporal mechanisms, or the τ-guide is updated after movement onset as a result of feedback relating to required effort.

The representation of required effort was also studied by McCloskey et al. (1974) who assessed the perceived heaviness of weights. They demonstrated that in a state of fatigue subjects overestimated the weight of a reference object, and concluded that a greater force was centrally generated in order to overcome the fatigue. Interestingly, Holmes (1922) showed a similar effect with patients with unilateral cerebellar lesions. When asked to use their affected arm to pick up a weight that matched a reference they overestimated and chose a weight that was heavier. Holmes concluded that in trying to compensate for the weakened muscles the patients overestimated the forces required. From this it would seem logical to suggest that if cerebellar patients tend to overestimate the force required to move their limbs, then the duration of a movement may also be misrepresented. If this is the case then the prediction would be that they would be less able to define appropriate durations for intrinsic τ-guides.

## 5.3 Predictions for the τ-coupling theory from the existing cerebellum literature.

From the literature reviewed above the predicted deficits in τ-coupling that would occur following cerebellar damage would include an inability to refine the estimated duration of an intrinsic τ-guide, and an inability to establish new patterns of simultaneous or sequential τ-couplings. Damage to the dentate nucleus would result in the use of inappropriate intrinsic τ-guides, while lesions to the interpositus

nucleus would create difficulties in movement execution. Tasks which involve visuomotor τ-couplings, and the integration and co-ordination of information from more than one sensory source are the most likely to be disrupted. An overestimation of the duration of an intrinsic τ-guide (due to an overestimation of required force) might be another possible deficit, and a general misrepresentation of movement duration might account for erratic movement patterns seen in many cerebellar patients.

From this discussion it would appear that every conceivable τ-coupling deficit could result from cerebellar damage. Hopefully, an analysis of the τ-coupling behaviour demonstrated by a patient with a localised cerebellar lesion might help clarify this and provide further insights into the complex nature of this structure, and indeed, the applicability of the τ-coupling theory.

## 5.4 Investigations in τ-coupling in a human with cerebellar damage

### 5.4.1 Subject

A twenty seven year old male (AM) participated in the experiments. Eight years previously he had had an operation to remove a cystic tumour from his cerebellum. The cyst lay mainly to the left of the midline with a solid component on the right. The tumour was an astrocytoma and when it was removed part of his dentate nucleus was also removed. Following the operation a small area of the tumour was found to remain in the left hemisphere.

After some initial problems AM had made a good recovery. He was able to perform many functional tasks such as feeding and dressing and he had good speech

skills. While his gait and postural stability remained poor he was able to take up yoga and had demonstrated the ability to learn new perceptuo-motor skills. At the time of testing AM's voluntary movements appeared slow and somewhat jerky. He could not stand unaided, and found locomotion tasks such as crawling difficult.

Data were collected during three three hour sessions in which AM was very co-operative throughout, although he tired easily. Control data were provided by various healthy subjects as detailed below.

5.4.2 Previous studies

AM had previously participated in a series of movement control studies (Lee et al., 1994). A $\tau$ analysis of his reaching and pointing abilities revealed that he had impairments in terms of braking, and several hypotheses were tested to assess the nature of these impairments. These tests included the extent to which he was able to pick up $\tau$ information, his ability to use visual information to guide movements, and his ability to correctly perceive position using articular proprioceptive information.

His ability to pick up $\tau$ information was tested on an interceptive timing task in which AM was asked to hit a ball that was rolled towards him down an inclined track. The results revealed that the timing of the onset of his actions was very similar to that of healthy controls, even though his movement patterns were less controlled than healthy counterparts. It was concluded that he had retained the ability to pick up $\tau$ information that allowed him to make appropriately timed actions.

The extent to which his impairments were due to deficits in visual guidance was assessed by asking him to perform a variety of tasks with his eyes open and

closed. It was found that his performance was poor in both conditions and it was concluded that he had deficits in both visual and non-visual guidance of movement.

The degree to which his impairments were based on an inability to adequately perceive position information using the articular proprioceptive system was also investigated. In a task where AM had to position his unseen hand under either a seen target, a felt and seen target, or just a felt target, he performed normally. It was concluded that his perception of position arising from articular proprioception or visual information was normal, and he was able to use information relating to his head and eye positions to sustain an accurate internal representation of egocentric space.

The overall conclusion from these studies was that AM did not have a generative perceptual deficit, but he had a marked inability to take up perceptual information to guide his actions on-line.

### 5.4.3 Predicted τ-coupling deficits for AM

From the timing of action shown in the ball hitting task it appeared that AM had retained the ability to use an extrinsic τ-guide to control his actions, but while his coupling was effective it was less consistent than that of the healthy controls. As a consequence, it was decided that an in depth analysis of intrinsically driven τ-couplings would be undertaken, and this seemed particularly appropriate given his dentate nucleus damage. The experiments were designed to assess the following questions;

1. Did AM's movements demonstrate the use of an appropriate intrinsic τ-guide?

2. Did he have an accurate mental representation of movement duration?
3. Was he able to exhibit behaviour that demonstrated τ-coupling?
4. Did his ability to demonstrate complex τ-couplings diminish when the perceptual load was increased?

## 5.5 The use of τ-guides and the temporal representation of movement durations

### 5.5.1 Introduction

There were three aims to this investigation; the first was to assess the role of the cerebellum, and in particular the dentate nucleus, in the generation and use of an intrinsic τ-guide in a reaching task. The second was to assess AM's performance on a reaching task where the gap was visually defined but the movement was executed without vision, and the third aim to was assess his ability to mentally represent the duration of a reaching movement.

If the dentate nucleus is involved in setting up an appropriate τ-guide then AM should have demonstrated comparable deficits on visual, non-visual and imagery tasks. Strong τ-couplings for visual and non-visual reaching movements should be evident but the movement durations should be variable in both. The generation of an inappropriate τ-guide should result in his movements being relatively smooth but inaccurate. AM should also be inaccurate when imagining the duration of a movement, with an overestimation of the movement duration possibly signifying a perceptual deficit related to the loss of muscular strength. That is, following the line of reasoning of McCloskey et al. (1974) and Holmes (1922), it is possible that,

compared to a control subject, AM might predict that movements would take longer since he perceived himself as being weaker than he actually was.

Finally, if AM was able to generate an intrinsic τ-guide, then his performance on the visual and non-visual tasks should be similar since only the τ-guide would be required for the prospective control of any kind of movement.

5.5.2 Method

In the first session AM was asked to perform a pointing task with and without on-line visual control. He was seated at a table and was told that his task was to move the index finger of his dominant right hand from a start point to a target that was located either 10cm, 20cm or 30cm horizontally to his right. He was asked to perform these movements with his eyes open or closed, and he completed a total of thirty six trials, corresponding to six trials in each condition. The movement of his finger was recorded using the Selspot system described in Chapter 3, with the camera being mounted above the table so that the x axis of its image plane was parallel to the plane of the horizontal movement. All trials were also recorded on video.

In the second session AM was asked to perform a mental chronometry task based on the same movement. He was seated at the same apparatus and placed his index finger on the start point where it stayed during the trials. He was then told which target he was to 'aim' for and, having looked at this target, he was instructed to look at his finger and close his eyes. He was told that on the command 'go' he was to imagine his finger moving from the start point to the target and to open his eyes the instant his finger reached the target. He was allowed three 'warm-up' trials

with vision (one to each location) before he completed six trials for each of the three distances. The time at which he opened his eyes, signifying arrival, was recorded onto video tape. A healthy twenty-four year old male acted as a control subject, and completed the same number of trials in each condition as AM.

5.5.3 Results

(a) Visual and non-visual reaching

Intrinsic τ-guides were calculated for the reaching movements and the nature of the τ-couplings between the intrinsic τ-guide and the movement τ ($\tau_{Finger\text{-}Target}$) was assessed. AM showed little evidence of τ-coupling. Data in Table 5.1 show that the mean percentage of the movement time for which AM τ-coupled did not reach thirty percent in any of the conditions. In comparison the control subject demonstrated an intrinsic τ-coupling for a significantly greater percentage of the movement time (eyes open $t_{(34)}=25.521$ $p<0.001$, eyes closed $t_{(34)}=22.080$ $p<0.001$), and on average the control's τ-couplings lasted for more than eighty percent of the movement duration.

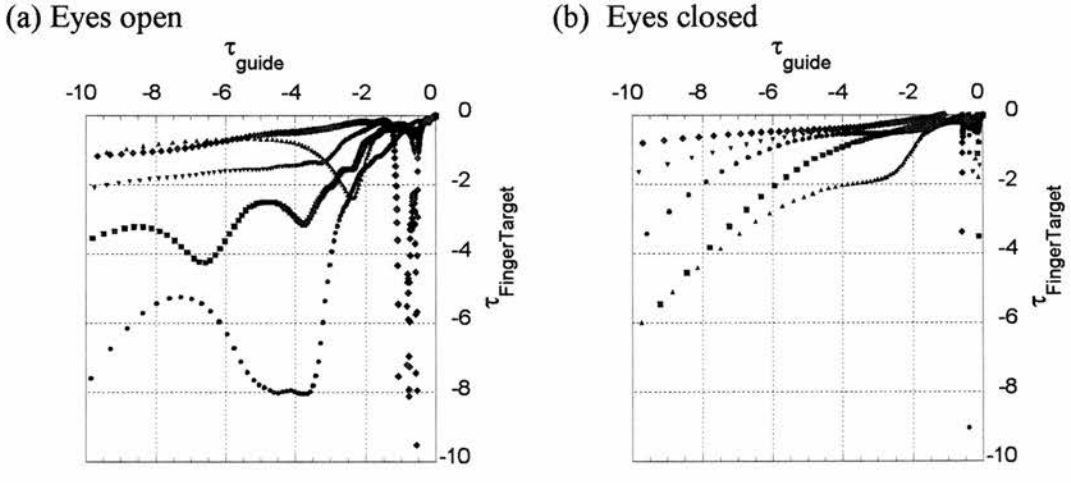



Figure 5.1 Composite plots of τ-couplings for AM with his (a) eyes open and (b) eyes closed for a 20cm reach.

While AM had a very apparent τ-coupling deficit on this task, qualitatively his performance improved without vision. As Figure 5.1 illustrates without vision his movements were less variable.

| | Open | | Closed | |
|---|---|---|---|---|
| **AM** | duration | % mt | duration | % mt |
| 10 cm | | | | |
| mean | 957.33 | 28.78 | 1059.25 | 26.69 |
| sd | 207.38 | 8.05 | 148.83 | 9.06 |
| 20 cm | | | | |
| mean | 1166.53 | 20.12 | 866.00 | 27.57 |
| sd | 154.07 | 9.26 | 69.88 | 10.90 |
| 30 cm | | | | |
| mean | 1867.47 | 18.45 | 1009.39 | 21.71 |
| sd | 26.57 | 7.44 | 23.56 | 7.28 |
| | | | | |
| **Control** | duration | % mt | duration | % mt |
| 10 cm | | | | |
| mean | 526.50 | 92.56 | 534.17 | 87.45 |
| sd | 40.84 | 5.50 | 57.08 | 8.60 |
| 20 cm | | | | |
| mean | 592.83 | 85.68 | 604.67 | 87.22 |
| sd | 28.33 | 8.36 | 63.36 | 7.74 |
| 30 cm | | | | |
| mean | 723.67 | 92.10 | 744.33 | 85.06 |
| sd | 90.50 | 3.81 | 70.98 | 7.42 |

Table 5.1 Means and standard deviations for the movement durations (ms) and percentage of the movement times for τ-couplings.

(b) The mental representation of movement times

From the time code on the video recordings the durations for overt and imagined movements were determined. These were then compared using t-tests and

the results are summarised in Table 5.2. From Figure 5.2 it can be seen that significant differences in AM's performance occurred due to an overestimation in the duration of imagined movements for the 10cm and 20cm conditions, but not in the 30cm condition. In all three conditions his performance when imagining movements was very variable (10cm sd=986msec, 20cm sd=1374msec, 30cm sd=1387msec), and it was interesting to note that he imagined the duration of the larger movements to be shorter than the durations of the smaller movements, although this was not significant (difference between the imagined durations of 20cm and 30cm movements $t_{(10)}$= 1.560 p=0.150, and between 10cm and 30cm movements $t_{(10)}$= 1.425 p=0.184). The control subject on the other hand imagined the 10cm movement to be significantly shorter than the 20cm movement ($t_{(10)}$=2.64 $p<0.05$) and the 30cm movement ($t_{(10)}$=4.48 $p<0.05$).

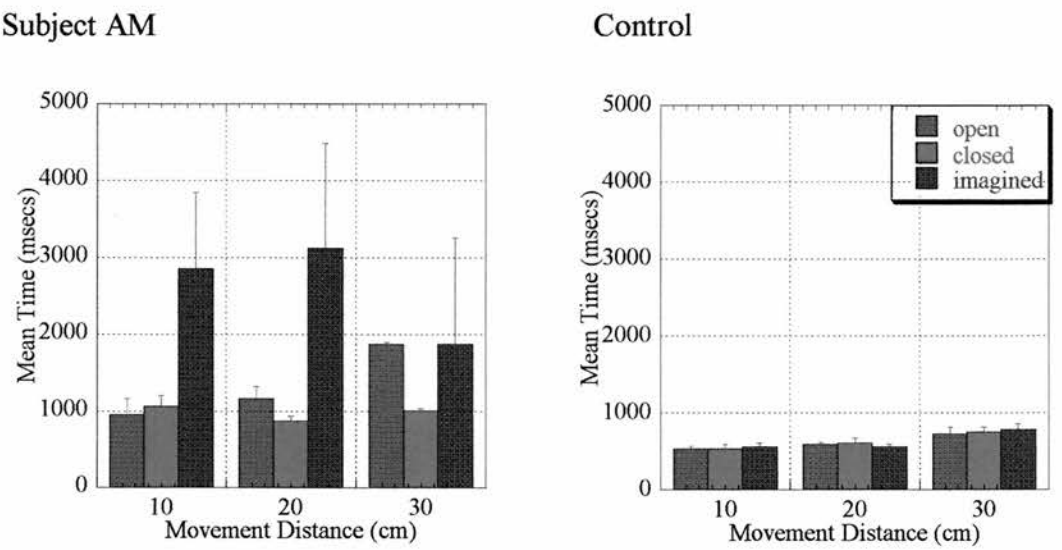



Figure 5.2 Means and standard deviations for the durations of real and imagined movements for AM (left) and control (right).

| | 10 cm | | 20 cm | | 30 cm | |
|---|---|---|---|---|---|---|
| | t value | p | t value | p | t value | p |
| AM open | 4.623 | 0.001 | 3.448 | 0.006 | 0.001 | 0.997 |
| AM closed | 4.421 | 0.001 | 3.999 | 0.003 | 1.498 | 0.165 |
| Control open | 0.972 | 0.354 | 1.829 | 0.097 | 1.205 | 0.256 |
| Control closed | 0.610 | 0.556 | 0.565 | 0.158 | 0.656 | 0.400 |

Table 5.2 Summary table showing results of t-tests between durations for imagined movements and actual movements made with and without vision at three distances.

5.5.4 Conclusion

AM showed a gross impairment in his ability to τ-couple in both the visual and non-visual pointing tasks. He was also less accurate in his ability to imagine movement durations, particularly when the extent of the movement was small. These results indicate that AM's deficit was not one in which he chose an inappropriate duration for an intrinsic τ-guide, but was more likely to be a fundamental deficit involving the generation or use of an intrinsic τ-guide.

The results from the mental imagery task suggested a disordered mental representation of movement duration, although this must be viewed with caution since it is possible that during the imagined task he was exhibiting a motor deficit relating to the opening his eyelids. However, since Nichelli et al. (1996) have shown perceptual timing deficits on discrimination tasks in patients with cerebellar degeneration it is likely that a considerable part of the variance shown by AM in this task was due to a central rather than peripheral deficit. It seems unlikely that his

tendency to overestimate imagined movement durations was a reflection of a misperception of muscular strength since he did not consistently overestimate in all the situations. It would not be logical to suggest that he would overestimate the duration of a small movement but not a large movement. However, it could be argued that his inability to estimate the duration of the small movements indicated that his deficit was time dependent. Clarke et al. (1996) proposed that cerebellar impairments are more evident for short as opposed to long duration tasks. However, during the overt movements AM's mean duration for the 30cm movements differed considerably between the vision (mean =1867ms) and non-vision (mean=1009.39ms) conditions, so the suggestion that AM was better able to determine the duration of a longer τ-guide can only be offered as a tentative conclusion. A more likely conclusion is that his disordered temporal representation of movement duration indicates that he is not able to generate a time dependent process, such as a functional τ-guide.

The fact that AM's ability to τ-couple improved without vision indicates that he was not using an internal-proprioceptive coupling, or that if he was, then vision was somehow acting as a disrupting influence. However, it is possible that poor processing of visual information was central to all the deficits AM showed in this investigation since in all three tasks visual information was used to define the gap. In order to assess whether this could be the fundamental basis of AM's possible inability to generate or use an intrinsic τ-guide an investigation of a proprioceptively guided movement was undertaken.

## 5.6 The use of an intrinsic τ-guide in a proprioceptively controlled action.

### 5.6.1 Introduction

Since his operation AM had taken up yoga and had become proficient at performing a series of relatively slow gross body movements. The aim of this investigation was to assess AM's ability to use an intrinsic τ-guide in a task that was not defined or controlled visually, so the use of a yoga movement seemed appropriate.

### 5.6.2 Method

AM lay on his back on the floor and performed a series of movements where he raised both legs together from the floor to the vertical and then back to the floor, his legs being kept straight throughout. His head remained on the floor and he fixed his gaze on the ceiling. IRLeds were placed on his right hip and ankle, and a Selspot camera mounted on a tripod 10cm from the floor was positioned so that its optical axis was perpendicular to the plane of movement. Since his upper torso remained on the floor throughout the experiment the leg movements caused a flexion or extension of the hip angle. A healthy adult who practised yoga acted as a control.

### 5.6.3 Results

The hip angle was defined as the angle between the horizontal line through the hip IRLed and the line between the hip and ankle IRLeds. Intrinsic τ-guides and movement τs were calculated for flexion (upwards movements) and extension

(downwards movements) of the hip angle and an analysis of the τ-coupling, as described in Chapter 3, was undertaken.

(a) Flexion of the hip angle

AM's performance for the flexion of the hip angle did not significantly differ from the control subject in terms of the percentage of movement time τ-coupling existed for ($t_{(10)}$=0.447 p=0.664), or the variance that the linear regression accounted for ($t_{(10)}$=0.768 p=0.460).

| | k | $r^2$ | coupling duration (ms) | % mt coupled |
|---|---|---|---|---|
| AM Flexion of Hip Angle | | | | |
| mean | 0.59 | 0.99 | 1635.42 | 99.34 |
| sd | 0.04 | 0.01 | 177.08 | 0.75 |
| Control Flexion of Hip Angle | | | | |
| mean | 0.49 | 0.98 | 1957.29 | 99.13 |
| sd | 0.13 | 0.01 | 228.83 | 0.87 |
| AM Extension of Hip Angle | | | | |
| mean | 0.54 | 0.98 | 2072.40 | 77.99 |
| sd | 0.19 | 0.01 | 284.12 | 12.58 |
| Control Extension of Hip Angle | | | | |
| mean | 0.22 | 0.98 | 2773.96 | 97.00 |
| sd | 0.04 | 0.01 | 193.34 | 1.93 |

Table 5.3 Means and standard deviations for the τ-coupling constant k, the $r^2$ values for the coupling regression, and the percentage of movement time where τ-coupling occurred.

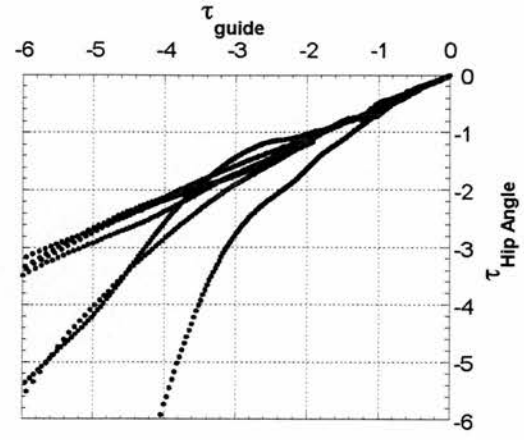
As shown in Table 5.3 AM demonstrated a τ-coupling between an intrinsic τ-guide and a movement τ which lasted on average for 99.13% percent of the

movement included in the analysis. However, he did slightly differ from the control in terms of strategy. AM's mean value of k was 0.589 while the control's was lower at 0.490. This difference was not significant ($t_{(10)}$= 1.814 p=0.099), and, as shown in Figure 5.3, AM was more consistent in his coupling strategy (k) than the control (AM sd=0.042 control sd=0.126).

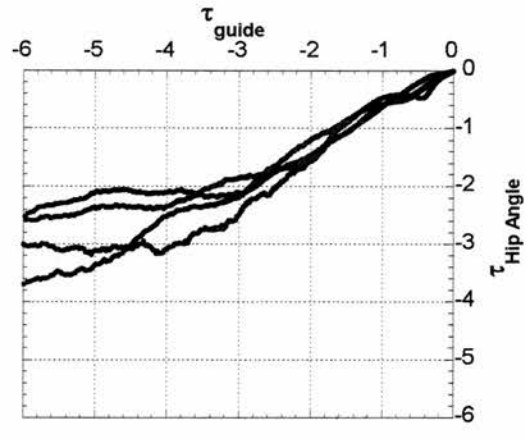
(b) Extension of the Hip Angle

Since the extension movement involved an eccentric contraction it was not surprising to find that AM's control was less precise than in the flexion movement (Table 5.3 and Figure 5.3). However, he still exhibited a τ-coupling for an average of 77.99% of the movement even though his performance was significantly worse than the control's (control mean=97.00% $t_{(10)}$=3.661 p=0.004). AM showed a greater variability in his τ-coupling, (standard deviations percentage of coupling duration AM=12.58 control sd=1.93) and he had significantly higher values of k ($t_{(10)}$=3.960 p=0.003) than the control. This more abrupt stopping strategy was a possible indicator that AM's abdominal muscles were comparatively weaker than the control's.

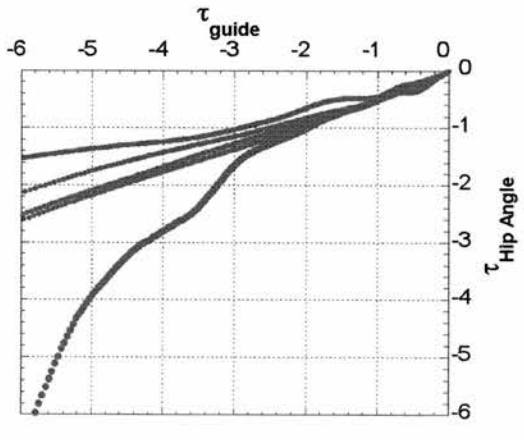
(a) AM Flexion




(b) AM Extension




(c) Control Flexion




(d) Control Extension

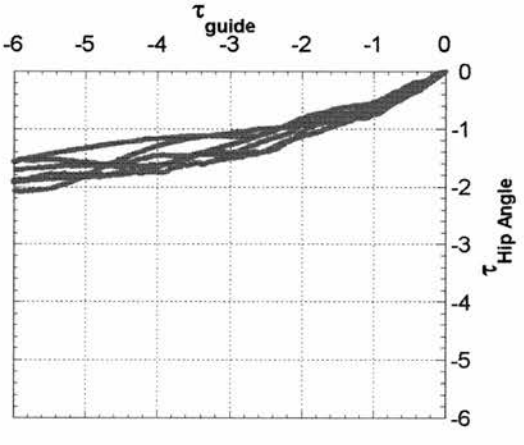



Figure 5.3 τ–coupling plots for AM and the control subject. Left panel (a and c) show flexion movements of the legs and the right panel (b and d) depict extension movements.

5.6.4 Conclusion

It was concluded from this investigation that AM could effectively generate and use an intrinsic τ-guide to control a gross proprioceptively guided movement.

## 5.7 The use of an intrinsic τ-guide in the coordination of a movement composed of two sub-movements.

### 5.7.1 Introduction

Results from the previous two investigations suggest that poor visual information had a detrimental effect on AM's ability to demonstrate τ-coupling. Using vision to define a gap in tasks such as the reaching task used in experiment 5.5 will inevitably involve the use of eye movements, and in particular saccades. Poor oculomotor control could contribute to this deficit so the first aim of this investigation was assess AM's gaze movements for indication of τ-coupling behaviour. The second aim was to assess if AM had a deficits on a complex co-ordination task, and gaze shifting was chosen since it provided an intricate level of co-ordination.

The output signal from the superior colliculus is thought to code a gaze movement which is then decomposed into head and eye movements (Phillips et al., 1995), so the task of gaze shifting could involve the generation of a single intrinsic τ-guide for gaze onto which head and eye movement τs could be coupled at different times. Results from the previous investigations indicated that it was unlikely that AM would perform well on a gaze shifting task, however, since the gaze shifting involved controlling two elements (head and eye) which are not be simultaneously τ-coupled to each other (because the relative contributions of each differ according to orbital eye position), one aim of the investigation was to ascertain if AM's deficit would lie in the control of the head movement, the eye movement, or both.

Miles (1991) suggested that the role of the cerebellum in the control of saccades is in establishing and maintaining accuracy, rather than programming, and this would lead to a prediction that the ability to establish the duration for an intrinsic τ-guide would remain unaffected following cerebellum damage, but the τ-coupling mechanisms that co-ordinate head and eye movements would be disrupted. However, while the vermis has been credited with controlling the pulse size and the hemispheres the holding step of eye movements (Optican and Robinson, 1980 Zee et al., 1981), the metrics of saccades in cerebellar patients are thought to be normal (Optican and Robinson, 1980). This would tend to support an opposing prediction, that is one in which τ-coupling is intact and there is a deficit in defining the duration of an intrinsic τ-guide.

The cerebellum's involvement in gaze movements has attracted less attention, although its role in vestibulo-ocular reflex has been well documented (especially with respect to the regulation of long term gain). However, the research on saccades indicates that the cerebellum also has a role in the control of gaze movements.

The experiment in Chapter 4 established that healthy adults are able to co-ordinate their head and eye movements to shift their gaze to a target, and it was found that the coupling between the effector τ ($\tau_{Gaze\text{-}Target}$) and an intrinsic τ-guide was dependent on being able to determine the duration for the guide. A similar paradigm was used in this investigation to assess AM's gaze shifting abilities.

### 5.7.2 Method

The apparatus used in this experiment was the same as that used in the experiment described in Chapter 4. During the first experimental session AM was

asked to make large gaze shifts to a moving target. He found this task difficult and was unable to complete it successfully. In a subsequent session AM was asked to perform a simpler task, that of making a large gaze shift to a known stationary target.

Prior to the experiment several recordings of AM's eye movements were taken to assess his general oculomotor function. During a slow tracking task it was noted that his pursuit was broken, and he had intrusive square wave jerks. When asked to hold his eyes away from the midline he showed no signs of gaze evoked nystagmus. Using electro-oculography to record his eye movements, and the Selspot system to record his head movement, AM was asked to make gaze shifts to stationary targets placed at different positions on the track, as shown in Figure 4.2. There were two conditions; visually driven and remembered gaze shifts. The visually driven movements were in the range of sixty to seventy degrees, and the remembered one hundred and forty to one hundred and fifty degrees.

A healthy twenty five year old male acted as a control subject, and both subjects completed twelve trials in each of the two conditions. There were equal numbers of leftwards and rightwards movements and the trials were presented in a random order. Data were collected in the same manner to that described in Chapter 4, and since no asymmetries were found for either subject, leftwards and rightwards movements was pooled. Intrinsic $\tau$-guides were calculated for each gaze shift, and the extent of $\tau$-coupling was used as a means of control was assessed.

5.7.3 Results

Figure 5.4 shows the disordered nature of AM's gaze control. He showed a tendency to undershoot and make multiple movements. In terms of the staccato nature of the velocity profiles his performance was worse for the larger movements (mean number of sub-movements = 5.00) than the smaller ones (mean= 2.55). Invariably during a trial AM's gaze would slow and then reaccelerate as opposed to stopping and re-starting. Most of his gaze shifts broke down after a preliminary eye movement, and unlike the control subject, AM appeared to be unable to 'fix' the orbital position of his eye and use his head to extend the gaze movement. This is shown quite clearly in Figure 5.5 where the $\tau_{Eye\text{-}Head}$ for the control subject is a smooth curve which ends prior to the head movement, but for AM the $\tau_{Eye\text{-}Head}$ is jerky and continues throughout the gaze shift.

Not surprisingly there was little evidence to indicate that AM was using a $\tau$–coupling strategy (Table 5.4). The mean time spent coupled was 64.8msecs for the visually driven movements and 65.7msecs for the remembered, but since the remembered movements were larger and, therefore, had a longer duration this represented 34.4% and 24.6% of the total movement time respectively. In contrast the control subject had couplings which lasted for approximately 80% the movement (60 degree shifts mean=81.75%, sd=6.5, and 140 degree shifts mean=80.89%, sd=9.6). The 'format' of the gap representation did not seem to alter the level of AM's control, in that the memory driven movements were as poorly controlled as the visually driven ones.

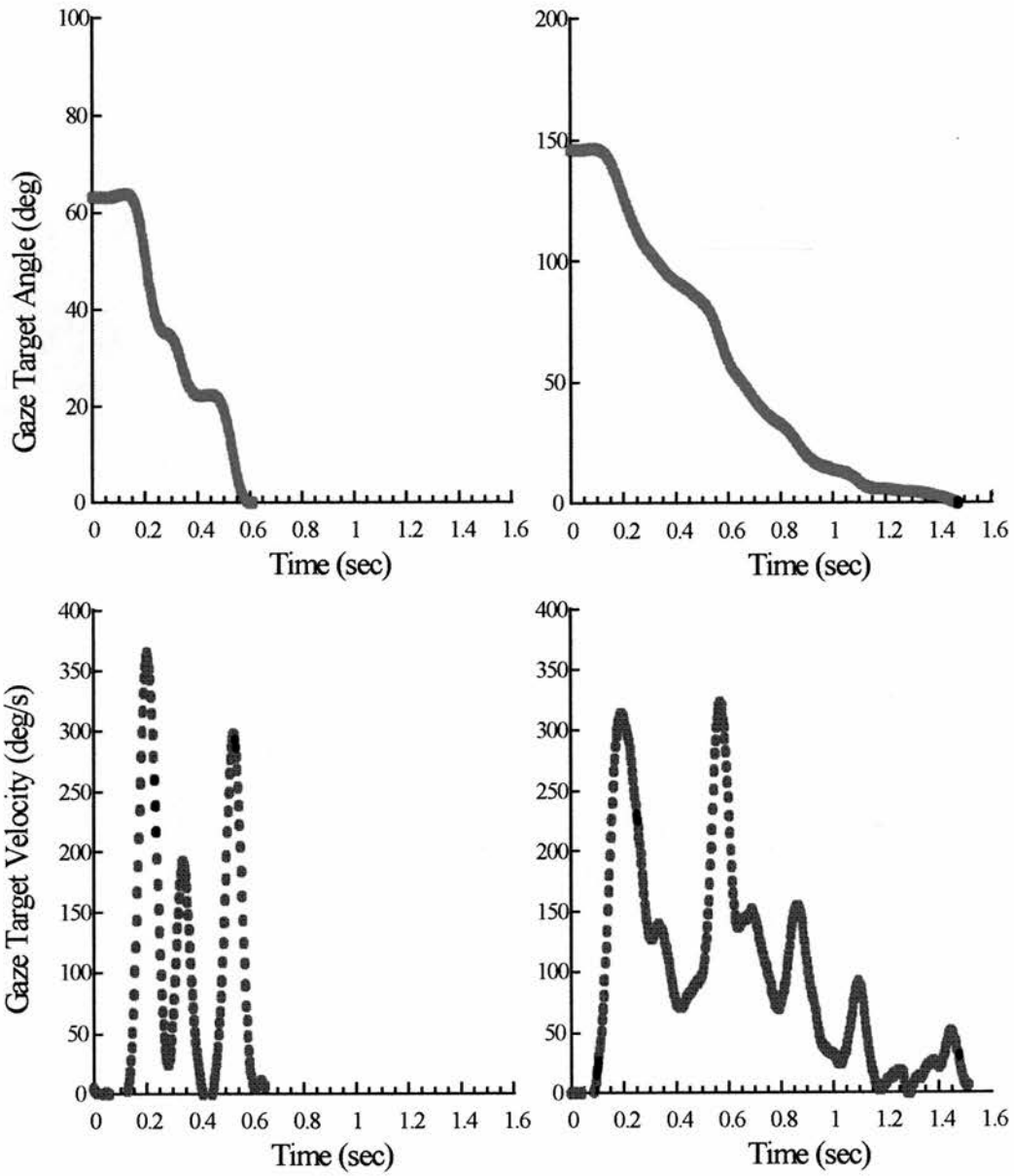



Figure 5.4 Typical gaze target position (top panels) and velocity profiles (bottom panels) for AM making a 62 degree gaze shift (left panels) and a 156 degree gaze shift (right panels).

| | k | $r^2$ | % mt coupled | coupling duration (ms) | gaze error | amplitude | duration |
|---|---|---|---|---|---|---|---|
| *60 Degree Gaze Shift to a Static Target* | | | | | | | |
| **AM** | | | | | | | |
| mean | 0.08 | 0.96 | 34.43 | 64.85 | 23.39 | 64.03 | 198.56 |
| sd | 0.02 | 0.00 | 17.74 | 28.04 | 10.48 | 3.10 | 54.08 |
| **Control** | | | | | | | |
| mean | 0.33 | 0.98 | 81.75 | 48.42 | 3.65 | 56.35 | 58.97 |
| sd | 0.13 | 0.01 | 6.50 | 14.60 | 2.07 | 2.07 | 16.75 |
| *140 Degree Gaze Shift to a Static Target* | | | | | | | |
| **AM** | | | | | | | |
| mean | 0.11 | 0.97 | 24.59 | 65.78 | 90.48 | 144.35 | 278.79 |
| sd | 0.02 | 0.01 | 7.70 | 7.86 | 18.27 | 6.59 | 44.35 |
| **Control** | | | | | | | |
| mean | 0.33 | 0.98 | 80.89 | 122.13 | 4.12 | 135.88 | 149.74 |
| sd | 0.15 | 0.01 | 9.76 | 28.93 | 2.52 | 2.52 | 23.43 |

Table 5.4 Summary data for gaze shifts for AM and control

The extent to which AM's deficit was related to either head or eye movements, or both was assessed by plotting the $\tau$ profiles for these two components separately. Figure 5.5 shows typical trials for AM and the control subject. Typically AM's $\tau_{\text{Eye-Head}}$ profiles were very broken and jerky, and to a lesser extent so were his $\tau_{\text{Head-Target}}$ profiles. Thus, there appeared to be little evidence to suggest that AM had a high degree control over either component.

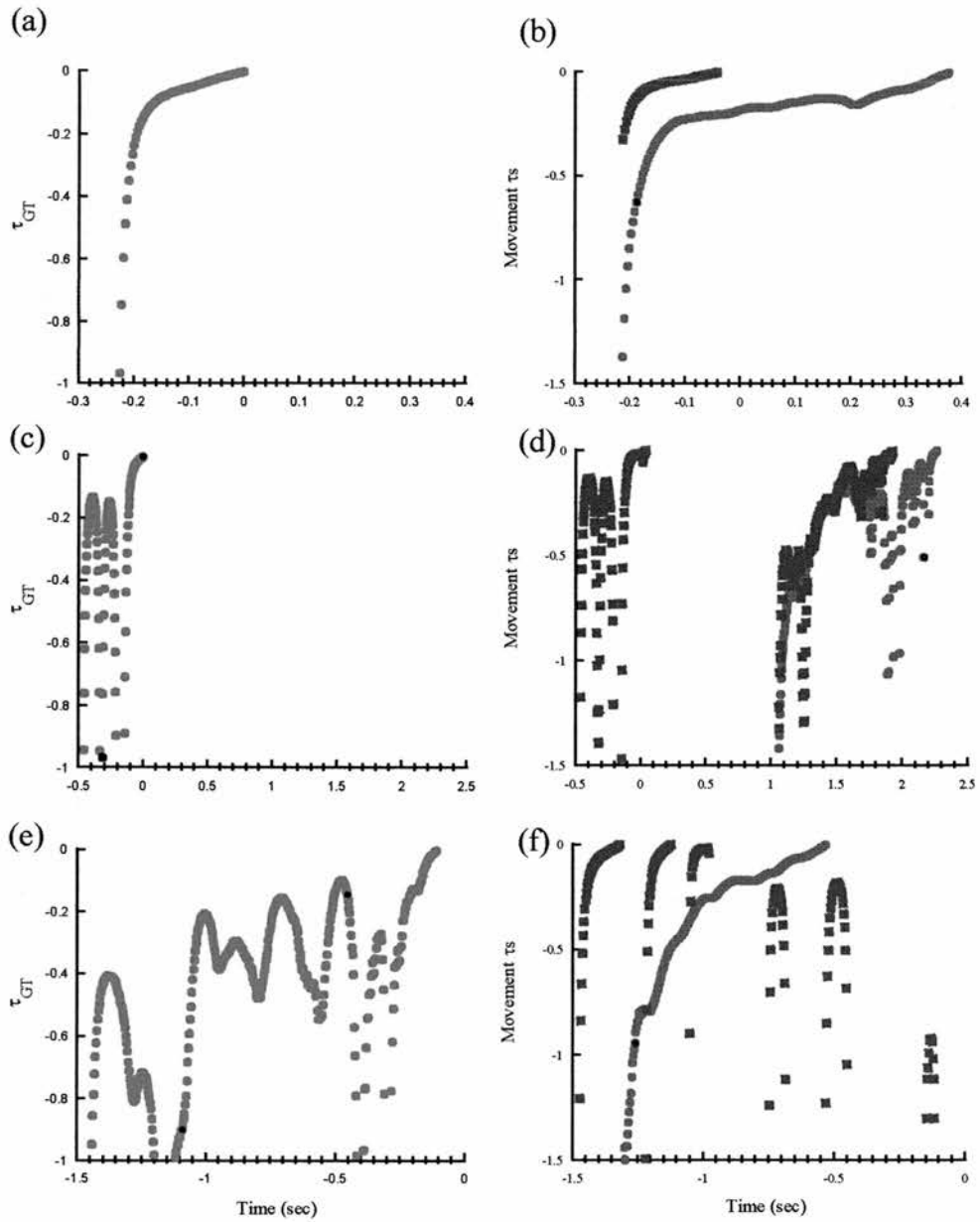



Figure 5.5 Left panels show the gaze-target τ plotted against time while the right hand panels show the head-target τ (blue) and eye-head τ (green). Plots (a) and (b) show a 140 degree gaze shift executed by the control. Plots (c) and (d) show a 60 degree movement by AM and plots (e) and (f) show AM making a 140 degree gaze shift.

5.7.4 Conclusion

AM was unable to use a τ-coupling strategy to control his gaze movements. He appeared to use his head and eyes separately rather than making co-ordinated gaze shifts. This suggests he was unable to couple his head and eye movements τs onto an appropriate intrinsic τ-guide. If AM had lost the ability to accurately perceive the force requirements, as Holmes' (1922) work would suggest, then he would have to make continual adjustments during the movement which could account for the jerky nature of AM's kinematic profiles. The fact that AM did not make a series of small movements with distinct pauses that would allow him to re-assess the remaining gaze-target angle, but periodically slowed then re-accelerated his gaze, suggested that he had a clear representation of the required move but was unable to issue the appropriate commands to achieve his goal. The intrusion of square wave jerks did not stop him from reaching his final goal which suggests that even initially his perception of egocentric space was intact. Together these findings suggest AM was not effectively using a pre-programmed intrinsic τ-guide since he had to make a series of on-line adjustments.

One other possible explanation for AM's poor performance on this task was that he was using an on-line visual control strategy to guide his movements, and it was this that was deficient. However, since the sixty degree movements were fast (mean duration=198.56 sd=54.08) this seems unlikely.

## 5.8 Multiple simultaneous τ-couplings

### 5.8.1 Introduction

The investigation into gaze shifting indicated that AM was unable to 'decompose' an effector τ into a co-ordinated sequential pattern of movement τs for two different body segments. However, since the investigation into yoga had revealed that he was able to control movements in a way that corresponded to the use of an intrinsic τ guide, it seemed that part of his deficit lay in the integration of multiple sources of information. To test this further an investigation into his ability to perform the hand to mouth task (Lee et al., 1998b) was undertaken. This paradigm provided a more complex task in which in healthy adults had demonstrated the control of two simultaneous τ-couplings; an intrinsic τ-guide coupled to a movement τ of the distance between the finger and the mouth, and a coupling between the τ of the distance and the τ of the angle of approach.

It was predicted that if AM's problem was essentially one in which he is unable to create or use an intrinsic τ-guide in complex situations then he should show greater deficits for the guide-movement τ-coupling than the movement-movement τ-coupling. However, if his problem lies in a more general inability to couple τs then both couplings show be affected to a similar degree.

### 5.8.2 Method

The method described in Lee et al. (1998b) was replicated in this experiment. Briefly, AM sat at a table and was asked to pick up a grape between the thumb and

index finger and raise it to his mouth. He did this sixteen times, eight with eyes shut and eight with eyes open, in random order, and on each attempt he tilted his head back to an unusual position, to assume a different angle of tilt on each trial. The movement of finger to mouth was recorded using a Selspot camera positioned 1.50m from the subject at a height of 0.70m with its optical axis perpendicular to the plane of movement of the finger. The camera recorded the (x,y) coordinates of three IRLeds attached to the finger, nose and chin respectively. Data was sampled at 312.5 Hz and filtered using a Gaussian filter with time constant sigma of 32ms. On each trial, the path of the finger relative to the mouth frame was calculated and the tangent of the finger's path just prior to the grape reaching its destination was determined and used to define a standardised head frame of reference. From this reference the distance and angle of the finger were calculated for the whole trajectory. $\tau$-couplings were assessed as previously.

5.8.3 Results.

Figure 5.6 shows the finger to mouth paths for AM with his eyes open and closed. In comparison to the healthy subjects (see Figure 1.2) AM's control appears to be much more erratic. This erratic behaviour was also reflected in the degree to which he exhibited $\tau$-coupling. Figure 5.7 shows that the percentage of movement time for which $\tau$-coupling occurred was greatest for the coupling between the intrinsic $\tau$-guide and the distance $\tau$, and was negligible for the $\tau$-couplings between the $\tau$-guide and $\tau$-angle, and the $\tau$-distance and $\tau$-angle.

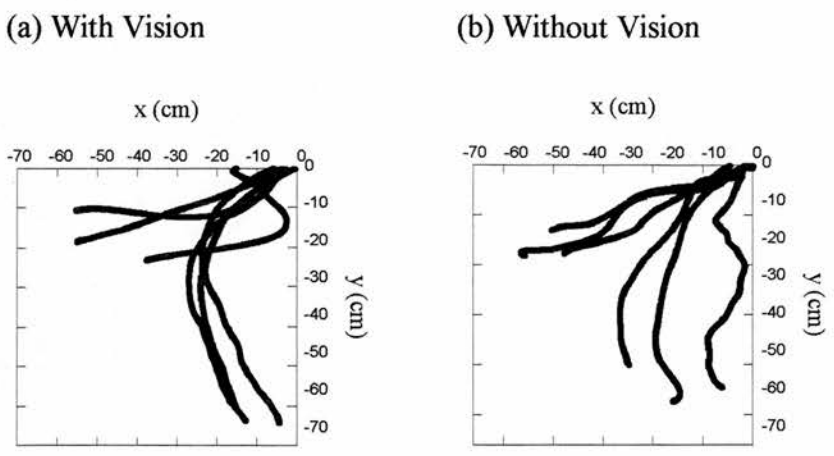



Figure 5.6 Paths of the finger to the mouth (0,0) for AM.

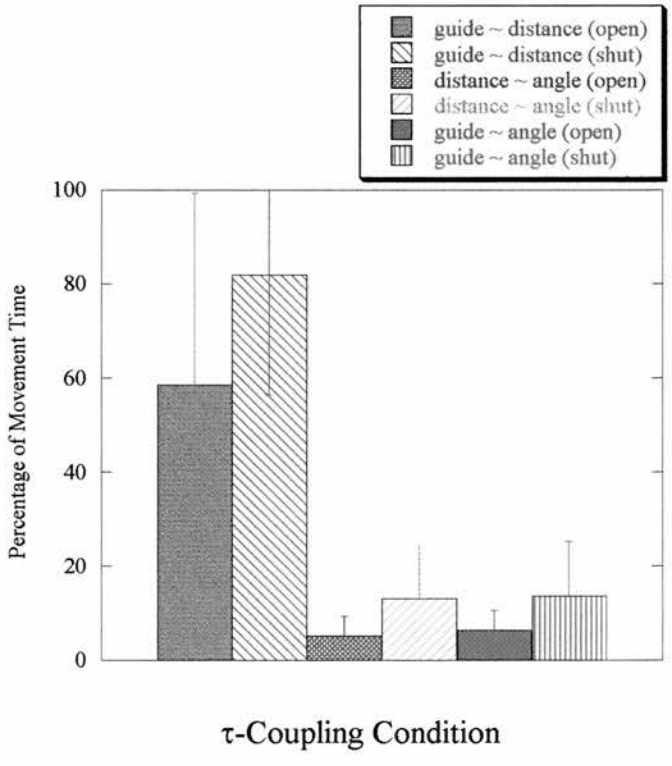



Figure 5.7 Graph showing the mean and s.d. of the percentage of movement time for which AM exhibited various τ-couplings. Solid bars indicate conditions where AM's eyes were open and the hatched bars conditions where his eyes were closed.

5.8.4 Conclusion

Without vision AM showed a relatively high degree of τ-coupling of the finger mouth distance onto an intrinsic τ-guide. This fitted with the notion that he was able to create and use an intrinsic τ-guide in a relatively complex non-visual situation. However, unlike the healthy adults he was unable to couple the finger mouth distance τ and the finger mouth angle τ, and consequently he did not demonstrate simultaneous couplings. This could reflect a general inability in directional control of movement, although given that this seems unlikely since he showed in investigation 5.6 that he could accurately control the flexion and extension of his hip angle. It seems more probable that AM's problem lies in a more general inability to couple τs and the deficits worsens as the perceptual load increases.

5.9 General Discussion.

From these studies it appears that AM was able to create and use an appropriate intrinsic τ-guide in certain situations that required his actions to be controlled proprioceptively. In more complex situations, especially those involving vision, his τ-coupling ability was compromised. This was particularly the case when he had to make simultaneous τ-couplings (hand to mouth) or complex non-simultaneous couplings (head and eye), suggesting that the area of the cerebellum that AM had damaged plays an important role in the co-ordination of τ-couplings.

In simple movements which involved vision the extent to which AM exhibited behaviour that indicated he was using an intrinsic τ-guide in a coupling

strategy was negligible. That is not to say that he was unable to achieve the movement goal, but his temporal control of action was severely disrupted. Occasionally, during a movement he would exhibit jerks which moved his limbs or eyes off in an unexpected direction, creating a kind of internal perturbation that had to be corrected. However, when this occurred he appeared to maintain an overall sense of the required end position even though he could not accurately control the timing and trajectory of his movements. This suggested that his strategy was more position based than $\tau$ based.

The damage to AM's dentate nucleus did not result in a deficit in defining the duration of an intrinsic $\tau$-guide for gross proprioceptive movements, but his need for on-line adjustments during tasks involving vision suggested that he had an inability to use an intrinsic $\tau$-guide. However, the fact that he was unable to accurately imagine the duration of his reaching movements suggests that vision disrupts the ability to define the duration of an intrinsic $\tau$-guide rendering this kind of control useless.

Overall, these studies suggest that the cerebellum has a complex role in producing movements that exhibit $\tau$-coupling. It is certainly involved in the integration of visual information that could be necessary for a $\tau$-coupling, or any other kind of coupling, in visually defined or guided actions. It also has a possible role to play in the use of appropriate intrinsic $\tau$-guides, although the fact that AM had $\tau$-coupling deficits in some but not all movements may reflect the locus of his injury.

# Chapter 6 : Generality of τ-coupling in Reaching Movements

## 6.1 Introduction

The previous two chapters have been concerned with the extent to which the τ-coupling theory is in agreement with what is know about the biology of the central nervous system. This is an important issue for the validation of any theory of natural behaviour, but there is also another issue of equal importance; that of generality. This chapter is concerned with assessing the degree to which intrinsic τ-couplings can be demonstrated in a variety of reaching movements.

As mentioned in Chapter 1 many criticisms of the τ theory have questioned its degree of generality. However, there appears to be some miscomprehension within the literature relating to the general theory. Bootsma et al. (1997) draw attention to the confusion concerning 'distinguishing specification from what is specified'. They make the point that movement τs and perceptual τs are not the same entities. Movement τs (sometimes called the τ margin) refer to the physical closures of gaps in an environment, while perceptual τs (referred to as τ) relate to the sensory information entering the brain or spinal cord. The confusion is compounded when authors, such as Wann (1996), fail to establish whether they are talking about perception or action. This lack of distinction, may not be an oversight of the authors, but may reflect their belief in the Gibsonian idea of a direct perception. Perhaps it is this that has led to the common assumption that τ theory predicts that there will always be a simple one to one relationship between a single source of perceptual information and the movement of an effector. Showing that this assumption limits

the range of actions to which the theory can be applied appears to have become a popular occupation for many experimenters, and has prompted a plethora of critiques (Tresilian, 1990, 1993, 1994, 1995, 1997, Wann, 1996, Smeets et al., 1996, Heuer, 1993). However, this has never been assumed in the generalised τ theory, although readers of the early studies (e.g. Lee, 1976) might be forgiven for gaining that impression. The restated and extended theory (Lee et al., 1998b) clarifies this question.

At present the empirical data in support of the τ-coupling theory only deals with movement τs. There is no data which conclusively shows that the perceptual τs from proprioceptive sources are perceived either directly or indirectly. In humans, however, this would not be easy to establish, since it would require recording afference during goal directed movements. If such a study was undertaken it would be invaluable to our understanding of perception-action τ-coupling, but in the meantime perhaps one way to extend our understanding is to assess the extent to which τ-coupling theory for movement is a good descriptor of motor control.

Regarding criteria for the demonstration of a τ-coupling the experiment on gaze shifting in Chapter 4 indicated that the subject must first be able to define the gap. Without this information the subjects of this experiment were not able to establish the τ-guide's duration (T). Given that the subjects were able to perform the task accurately, it was proposed that a τ-guide may be initiated during an on-going movement. However, since the durations of the possible τ-couplings were very short, no firm conclusions concerning this could be drawn.

Hypothetical velocity profiles of an effector that would result from an intrinsic τ-coupling ($\tau_{movement} = k\tau_{guide}$) were presented in Figure 1.1. These would suggest that movements must start and finish at rest. The extent to which this is a necessary condition will be investigated in this chapter. The other issue that will be addressed concerns to the idea that there may be invariants for the initiation of a τ-coupling, a concept which was introduced by Lee et al.'s (1981) study of diving behaviour in gannets. In relation to τ-coupling this idea was also raised in Chapter 4 where it was found that the mean duration for a τ-couplings in conditions where on-line visual control was needed was approximately 50msecs.

The task used in experiment described below was a reaching task in which reaches were made from both stationary and moving start points. The experiment was designed so that aspects of generality and criteria for τ-coupling onset could be investigated. Simple reaching actions have been used extensively by experimenters working on the problems of motor control and theories that have arisen from this work can be sub-divided into two different classes; engineering models and physiological models. The engineering models are based on optimisation principles such minimising kinetic energy, joint torques or jerk (the time derivative of acceleration, for example, Hogan, 1984) while the physiological models have considered how electromyographic patterns change with task parameters. The various models associated with the equilibrium point hypothesis described in Chapter 2 (page 22) fall into this category as do the models such as the speed control (Freund and Budingen, 1978) and the impulse timing hypothesis (Wallace, 1981). All of these model tend to share a common weakness; they are paradigm specific. They are difficult to test in dynamic unconstrained conditions and tend to ignore the role of

perception. The reaching task used in the present experiment was less constrained so that the τ-coupling theory could be assessed in a more naturalistic setting.

## 6.2 Method

### 6.2.1 Subjects

Six healthy right handed adults (mean age 25.6 years) volunteered to participate in the study.

### 6.2.2 Procedure

Each subject's task was to take a small plasticine ball (approximately 1.5 cm in diameter) between the forefinger and thumb of their right hand and drop it through a hole (3cm in diameter) in a box that was mounted on a pole at waist height. They were asked to do this in three different conditions. In the first the subject was stationary and stood at a comfortable distance from the box. In the second condition subjects were asked to walk slowly towards the box from a distance of approximately four metres, and drop the ball through the hole whilst they walked past. In the third condition they were requested to walk quickly towards the box and again drop the ball in the box as they passed. In the walking conditions the subjects were asked to hold the plasticine ball in front of them at a constant distance from their body. This was done to make measurements easier since it ensured that the hand could be tracked throughout the action. Each subject completed eight trials in each condition.

The subjects' movements were captured using a Selspot motion capture system and three IRLeds were used to monitor the x and y coordinates of the

subject's head (IRLed placed on the right temple), hand (IRLed placed on the nail of the index finger of the right hand) and target (IRLed placed on the top outer edge of the box perpendicular to the centre of the hole). The Selspot camera was positioned with its optical axis perpendicular to the plane of the subject's horizontal motion at a distance of 7m. This gave a field of view of 2.5m. The data was subsequently filtered using a fourth order Butterworth filter with a cut-off of 8Hz where the response had fallen by 3dB. The movement $\tau$ for the finger-target gap was then calculated from the start of the reaching movement to the time at which the goal was reached. The start of the movement was defined as the point at which the velocity of the gap between the head and finger first became non-zero, and the end of the movement when the finger-target velocity became zero. Since the measurement of movement $\tau$s becomes noisy at low velocities data corresponding to finger-target velocities of below 1cm/s were not included in further analyses. Typically, this resulted in data for the last 10ms of the movement being removed.

$\tau$-guides were calculated, and the effector $\tau$ (finger-target) was plotted against the intrinsic $\tau$ guide for each trial so that the extent and degree of coupling could be assessed.

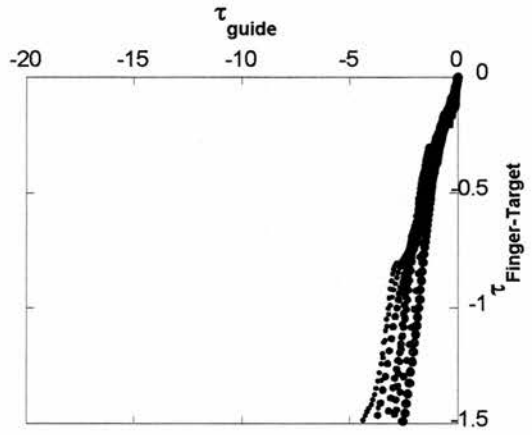
## 6.3 Results

### 6.3.1 Duration and strength of $\tau$-couplings

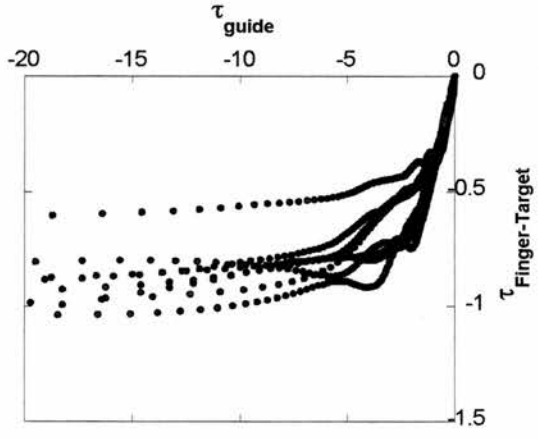
Figure 6.1 shows the $\tau$-$\tau$ plots for the intrinsic $\tau$-guide against the finger-target $\tau$ for one subject in the three conditions. It can be seen quite clearly from these that the degree of linearity differed dramatically between the stationary and

moving conditions. Reaches made under the stationary condition typically resulted in straighter plots than those made during locomotion.

(a) Stationary Reaches




(b) Slow Walk




(c) Fast Walk

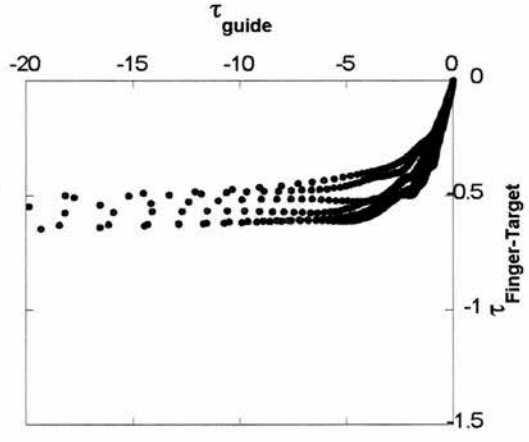



Figure 6.1 τ-τ plots for one subject in the three conditions

A one-way ANOVA on the percentage of the movement time accounted for by τ-coupling revealed a significant difference between conditions ($F_{(2,10)}$=103.70 $p<0.001$), and as shown in Figure 6.2 during the stationary reaches τ-coupling accounted for most of the movement (overall mean=93.39% s.d=4.06). A Tukey

HSD test showed this to be significantly greater than in the moving conditions where the duration dropped to under fifty percent of the movement time (slow walk overall mean=47.02% s.d.=7.87, fast walk overall mean=45.15% s.d.=10.21).

While the duration of τ-couplings differed between conditions the strength of the coupling (assessed by the $r^2$ value) was high in all conditions (stationary condition, mean = 0.990 s.d.=0.006, slow walk mean =0.988 s.d.=0.007, fast walk mean=0.988 s.d.=0.005).

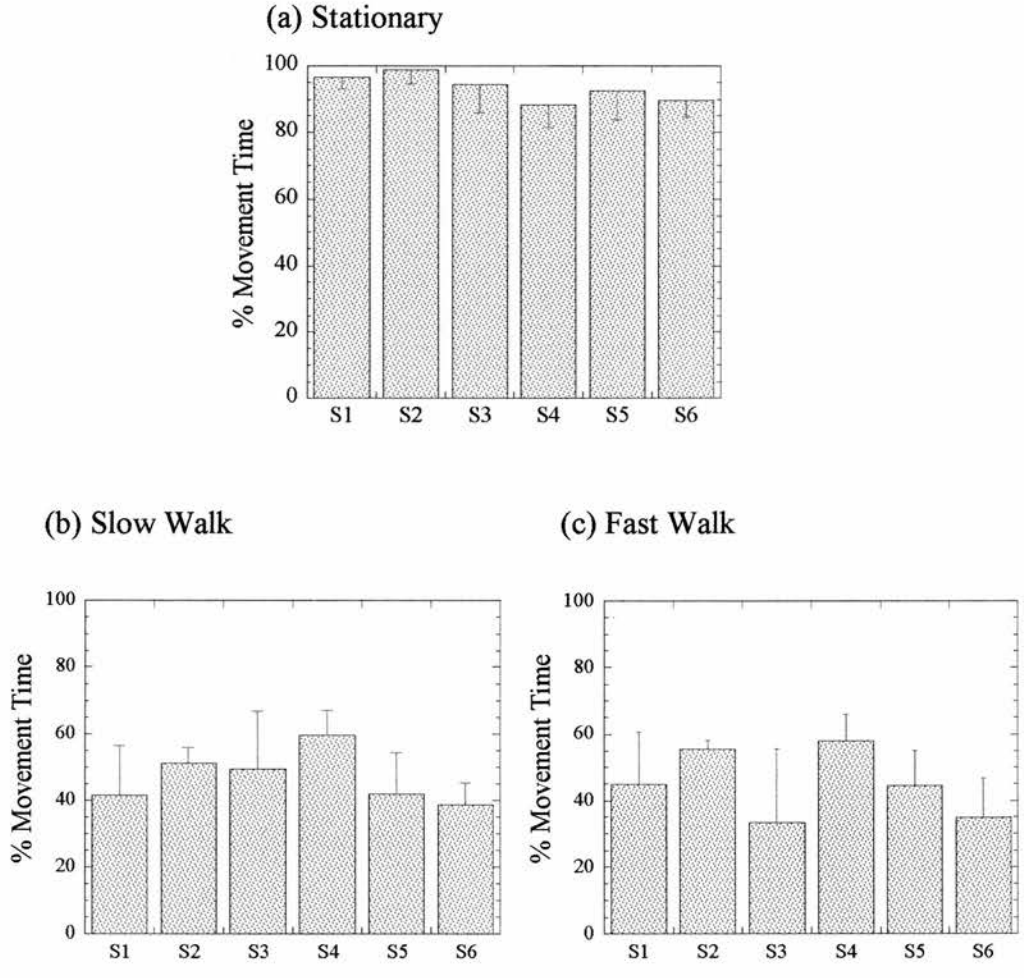



Figure 6.2 Percentage of movement time where an intrinsic $\tau_{guide}$ was coupled to $\tau_{Finger\text{-}Target}$ for all subjects in the three conditions.

6.3.2 Was the intrinsic τ-guide initiated prior to the reach onset?

Since it was evident that a τ-coupling did not exist from the time of reach onset in the walking conditions, it was hypothesised that the initiation of the τ-guide might occur prior to this time, during walking. It seemed logical to suggest that this could occur during the latter part of the locomotion approach phase, rather than at the start of the walking movement since, in theory, the initial approach could have been manipulated so that is was relatively unconnected from the reaching action (for instance, the starting position could have been in a location where the target box could not be seen). In order to test this hypothesis a series of τ-guides were calculated prior to the reach onset for trials in the walking conditions. That is, τ-guides were calculated which started every 3.125ms during the two second period prior to the start of the reach. These were then plotted against the finger-target τ and the strength and duration of these τ-couplings was assessed.

It can be seen from Figure 6.3 that changing the initiation time for the τ-guide had a dramatic effect on the shape of the curve and degree of linearity. However, when the duration of the coupling for each τ-guide was assessed using the recursive linear regression procedure described in Chapter 3 no differences were found for the time at which the τ-coupling started. This was analysed statistically by comparing a representative sample of τ-guides which corresponded to times t=0 (start of reaching movement), t=-100ms, t=-500ms, t=-1000ms and t=-2000ms. A one way ANOVA on the slow walk data revealed no significant differences in the coupling durations ($F_{(4,20)}=1.488$ $p>0.05$), and a similar result was obtained for the faster approach ($F_{(4,20)}=1.763$ $p>0.05$).

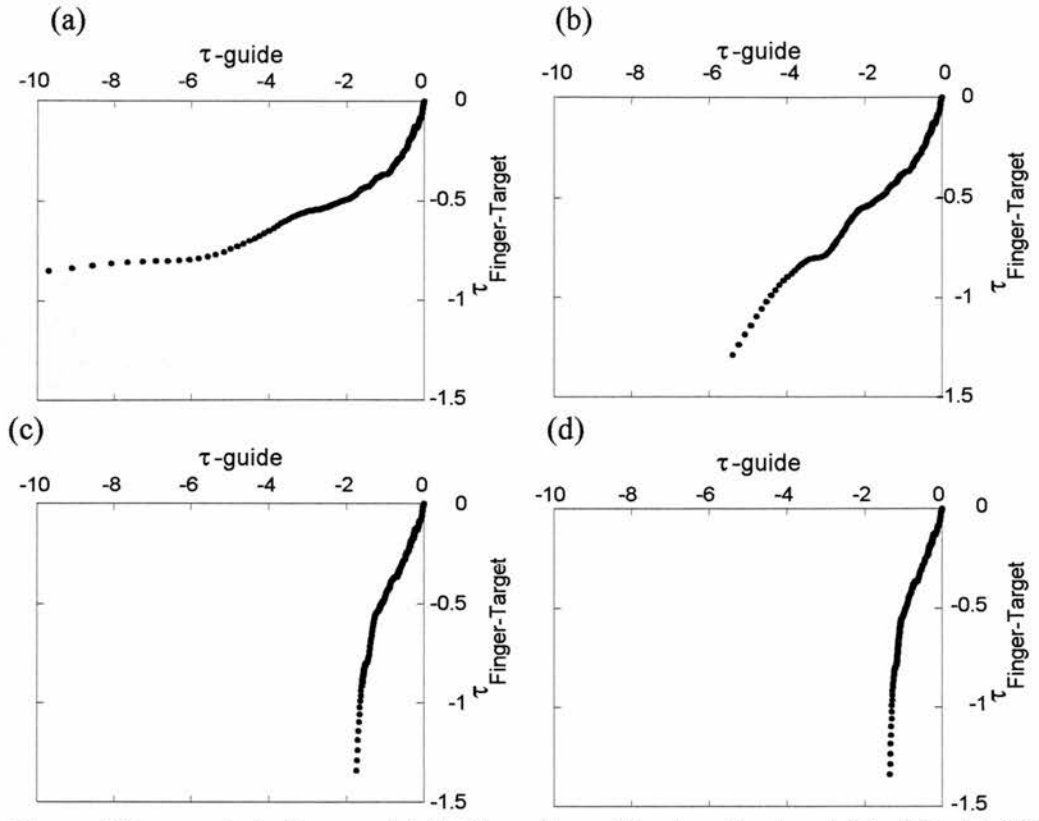



Figure 6.3 τ-τ plots for one trial where the subject walked quickly (S1, trial 9). In (a) the initiation of the τ-guide starts at reach onset (t=0). In (b) the τ-guide starts at 100ms prior to onset (t=-100), in (c) t=-500 and in (d) t=-1000ms.

6.6.3 Was there an invariant characteristic for τ-coupling onset?

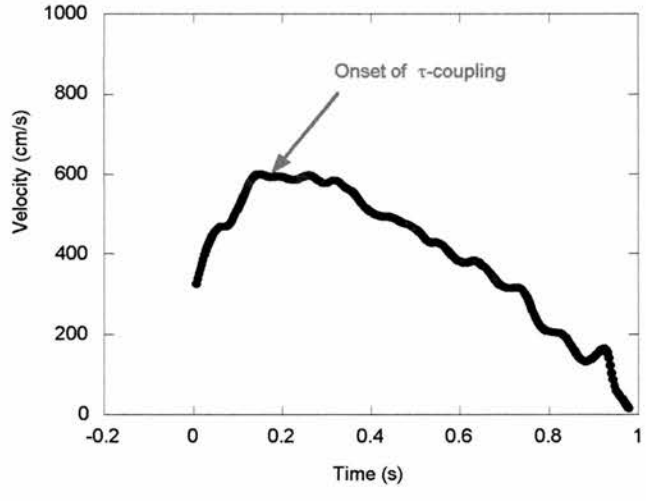



Figure 6.4 A typical finger-target velocity profile for one trial (S1, trial 9) in which the subject walked quickly.

The graph in Figure 6.4 indicates that the onset of τ-coupling in one trial where the subject was walking quickly was close to the point of peak finger-target velocity. To investigate the idea that there might be invariant characteristics that related to the onset of coupling, coefficients of variation were calculated for four parameters; finger distance from target, finger-target velocity, time to contact and the time of coupling onset in relation to peak finger-target velocity. While these coefficients are not directly comparable, it can be seen from Figure 6.5 that time to contact is the least likely control parameter, with little to distinguish between the other three candidates.

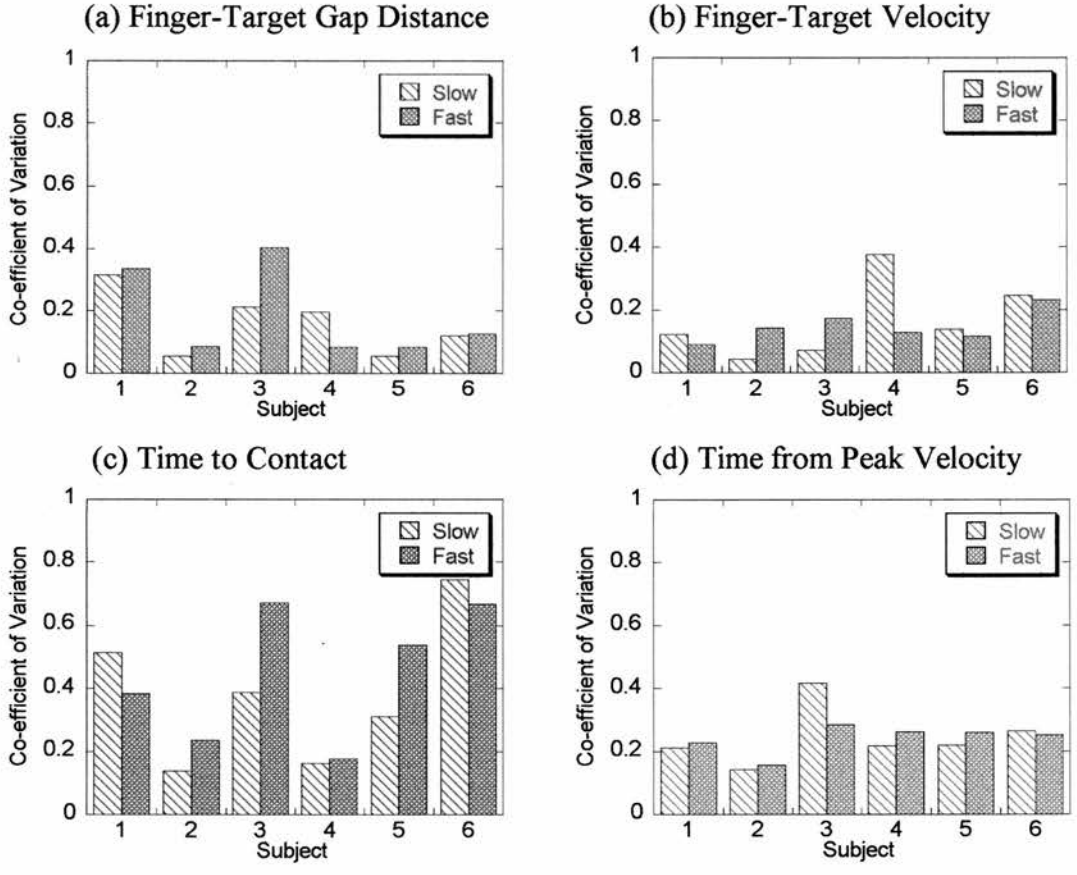



Figure 6.5 Coefficients of Variation for all subjects in both walking conditions. Plot (a) refers to the finger-target distance at coupling onset, plot (b) finger-target velocity, plot (c) time to contact and plot (d) the time duration between peak finger-target velocity and coupling onset.

## 6.4 Conclusion

The conclusion of this investigation has to be that the concept of intrinsic τ-coupling lacks generality when considering movements that do not start from rest. This is not surprising since the definition of an intrinsic τ-guide is that of a property that starts from rest and accelerates at a constant rate. However, future research might indicate that there are different types of τ-guide that could be used in different situations.

Additionally, the results do not provide any conclusive evidence that there is an invariant characteristic that signifies the onset of coupling. This may be because such invariants do not exist, or it could simply be explained by the fact that the subjects lacked consistency and based their performance on self-regulatory variables such as previous success, fatigue or level of motivation.

# Chapter 7: Conclusions

The aim of this thesis was to examine aspects of the generality and biological plausibility of τ-coupling theory. It focused on three different areas, the first of which related to oculomotor control. A study of shifts of gaze was undertaken to establish if the τ-coupling theory was congruent with known physiological data, and if it could provide an explanation for this behaviour. The second area considered was the possible role of the cerebellum in τ-coupling and a series of case studies showed that τ-coupling behaviour is disrupted in some, but not all, aspects motor control when this part of the brain is damaged. Finally, the extent to which the τ-coupling theory generalised to a serial movement was assessed in Chapter 6 where subjects performed a reaching task while walking.

## 7.1 Plausibility of the τ-coupling theory

Implicit in this theory is the idea that τ information provides the basic datum for neurological control mechanisms, and sensory organs relay τ information to the brain where an assessment of the required τ-coupling is made prior to the appropriate τ information being sent to the muscles. It provides an appealing account of how healthy humans can co-ordinate their actions in a variety of different situations. At the same time it suggests that the central nervous system might have two distinct timing mechanisms, one of which relates to the perception of external 'clock' time another which is concerned with the internal timing of action. This distinction between external and internal time seems appropriate given the research

showing that some cortical lesions result in distortions in 'clock' time while the co-ordination and timing of the actions of the lesioned subject remains normal. These findings have led to the further suggestion that the perception of 'clock' time is related to a dopaminergic mechanism within the basal ganglia (Boltz,1991, Pastor et al., 1992, Wogar et al., 1993). The τ-coupling theory, on the other hand, suggests that a timing mechanism related to movement and the consequential changes in sensory flow fields may also exist, and when this involves that use of an intrinsic τ-guide, this is based on constant acceleration.

The results from the experiment in Chapter 4 give support to the theory, and suggest how it might be further extended. It was argued that since there is evidence for representations that are not of the τ type within the central nervous system, the τ theory on its own cannot provide a complete explanation of the regulation or either perception or action. The movement-related activity of SLBNs in the brain stem provides a likely candidate for a correlate of a movement τ, but the representation of perceptual and intrinsic τs, if they exist, will involve 'higher order' neural structures. The results of the looking experiment also suggested that a 'lower level' τ-coupling may exist and indicated that the ballistic models of oculomotor saccadic control are inadequate descriptors of large gaze shifts. In this instance a direct perception-action coupling in oculomotor control could describe the behaviour. However, the τ-coupling models proposed to account for the gaze shifting (Figure 4.11, and Figure 4.12) predict that both direct and indirect information can be used in gap closures. This represents a shift away from the Gibsonian concept of direct perception-action coupling, although the theory remains fundamentally ecological in its outlook.

The extent to which possible mechanisms for τ-couplings could be related to the architecture of the brain, or to the firing rates of populations of neurons is still a matter of debate. At present it would appear logical to propose that the topographically mapped areas of the brain are involved in defining gaps, and neuronal firing rates relate to the kinematics of gap closures. This idea was central to the model proposed for the control of gaze shifts (Chapter 4). The experiments in Chapter 5 clearly indicate that the cerebellum also has an important role in the temporal control of action and in predicting the duration of movements.

The results from Chapter 5 showed that there were tasks, or aspects of task, in which the cerebellar patient AM had a high degree of τ like control, but others in which he did not. It may be concluded that any τ representation is unlikely to reside as a discrete entity within the central nervous system. Indeed, the disordered nature of AM's eye movements provides evidence that the cerebellum has an important input to the superior colliculus circuitry, and this is compatible with the conclusion that if intrinsic, perceptual or movement τs are represented neurally then it is likely that this representation will be distributed over many parts of the central nervous system.

## 7.2 Generality of τ-coupling theory

The constant acceleration intrinsic τ-guide hypothesis was proposed to account for movements which had a bell shaped velocity profile. This has provided the generalised τ theory with a strength that was missing from the earlier τ margin and $\dot{\tau}$ ideas. However, as the following discussion will indicate this strength is also a weakness.

The conclusion from this thesis is that the constant acceleration intrinsic τ-guide can only account for behaviour when several assumptions are met. The first of these is that the gap to be closed has to be defined in time and space before an effective intrinsic τ-guide can be used. The ability to do this was shown by some subjects when they shifted their gaze to an unknown target. The second assumption is that if τ-coupling is to account for a significant proportion of an action then that action must be discrete, that is it must start and end at rest. When actions do not meet this requirement, as in the experiment in Chapter 6, the theory has difficulty in describing the action. These two assumptions limit the range of behaviours to which this model can be applied, and reduce its power as a general theory of motor control. As with other theories, such as the equilibrium point hypothesis, this may be a reflection of the movements or actions that were used as a basis for establishing the mathematical model that forms the foundation of the τ theory.

The basic equation for an intrinsic τ-guide was based upon the fundamental law of motion

$$s = ut+0.5at^2 \qquad (10)$$

and the case when u=0 was taken to derive a relatively simple model. The result is that, in this form, the constant acceleration τ-guide describes an important but limited class of actions. If it is to account for other classes of movement then the degree of parsimony that can realistically be expected must be reduced.

The final assumption that needs to be met is that the movement duration can be accurately predicted. When a person is unable to do this τ-coupling is seriously disrupted, as AM demonstrated in the experiments described in Chapter 5. However, the fact that AM was still able to achieve a movement goal, albeit in an uncoordinated manner, suggests that when he could not use τ-coupling as a means of control he had other systems or strategies that he could use. This, again, indicates that the degree of complexity involved in natural motor control is greater than that envisioned by τ-coupling theory in its present form.

It is concluded that while the τ-coupling theory has advanced our understanding of how perception and actions might be integrated and controlled, and provides a unique way of thinking about these fundamental but difficult problems, the intrinsic τ-guide hypothesis in its present form does not describe a unifying fundamental law of behaviour. It has been shown to lack generality for non-discrete movements, and while it seems that τ like representations do exist in some form in the central nervous system there is still a long way to go before the biological plausibility of this theory can be established.

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# Appendix I

Constant Acceleration τ-guide

The theory (Lee et al., 1998b) states that at each time t during a self paced movement $\tau_m(t)$, the τ of the closing gap is coupled onto a τ-guide ($\tau_g$). Assuming that the guide corresponds to a quantity that starts from rest (t=0) and accelerates at a constant rate A until it reaches its goal level at time T, then the initial gap to the goal level will be $X_g(0)=0.5AT^2$. So after time t the gap will have reduced by $0.5At^2$ and

$$x_g(t)=0.5A(T^2-t^2) \quad (11)$$

The velocity of the gap change will be -At, so the τ-guide at the time t can be expressed as

$$\tau_g(t)=0.5A(t^2-T^2)/At \quad (12)$$

simplified as

$$\tau_g(t)=0.5((t-T^2)/t) \quad (13)$$

If the guide is coupled to a movement $\tau$ ($\tau_m$) then the $\tau$-coupling theorem states that

$$x_m(t)=Cx_g(t)^{(1/k)} \tag{14}$$

where C is a constant. By substituting $x_g(t)=0.5A(T^2-t^2)$ and differentiating with respect to time

$$\dot{x}_m(t)=-2D(1/k)t(T^2-t^2)^{(1/k-1)} \tag{15}$$

where D is a constant. By normalising equation (15) by setting the duration T=1, and the initial gap size $x_g(0)=1$

$$\dot{X}_m(t)=-2(1/k)t(1-t^2)^{(1/k-1)} \tag{16}$$

By substituting different values of k theoretical velocity profiles can be generated, and as shown in Figure 1.1 these have a bell shaped velocity profile.

# Appendix II

Calibration procedure for two Selspot cameras.

Since the two cameras had differing fields of view it was necessary to calibrate them. The cameras were set up so that their optical axes were parallel to a linear pole on which four IRLeds were placed at 50cm intervals (Figure A1).

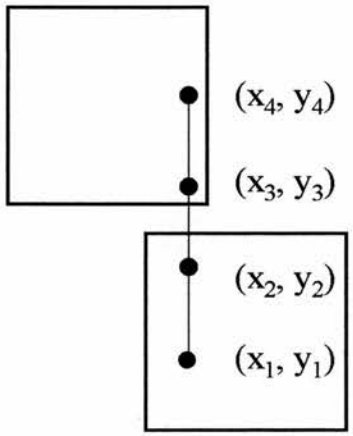


Figure A1 Diagram showing the two camera fields of view (□) and the placement of the calibration pole.

The cameras were calibrated as follows:

$$x_{cam1} = a + cX_{cam2} \quad (17)$$

$$y_{cam1} = a + cY_{cam2} \quad (18)$$

where a=shift in x, b=shift in y and c=relative gain.

Thus,

$$a = (x_1+x_2)/2 - c(x_3+x_4)/2 \quad (19)$$

$$b = 2y_2 - y_1 - cy_3 \quad (20)$$

$$c = (y_2-y_1)/(y_4-y_3) \quad (21)$$

# Appendix III

(a) Initial Gaze-Target Errors

| | KNOWN STATIONARY TARGET | | |
|---|---|---|---|
| | Mean Error | s.d | RMS Error |
| S1 | 3.535 | 7.600 | 8.112 |
| S2 | 7.430 | 5.256 | 8.973 |
| S3 | 2.814 | 7.562 | 7.829 |
| S4 | 2.082 | 4.117 | 4.480 |
| S5 | 4.159 | 5.630 | 6.857 |
| S6 | -0.724 | 6.190 | 5.970 |
| MEAN | 3.216 | 6.059 | 7.037 |

| | UNKNOWN STATIONARY TARGET | | |
|---|---|---|---|
| | Mean Error | s.d | RMS Error |
| S1 | 3.334 | 7.059 | 7.536 |
| S2 | 1.615 | 7.640 | 7.491 |
| S3 | 2.677 | 7.763 | 7.900 |
| S4 | 2.005 | 5.604 | 5.761 |
| S5 | 1.546 | 3.904 | 4.013 |
| S6 | -0.132 | 0.899 | 0.858 |
| MEAN | 1.841 | 5.478 | 5.593 |

| | CHASING | | |
|---|---|---|---|
| | Mean Error | s.d | RMS Error |
| S1 | 0.289 | 5.123 | 4.930 |
| S2 | 2.436 | 2.143 | 3.190 |
| S3 | 0.148 | 0.955 | 0.926 |
| S4 | 1.626 | 2.937 | 3.257 |
| S5 | -2.052 | 3.893 | 4.241 |
| S6 | -0.591 | 2.521 | 2.464 |
| MEAN | 0.310 | 2.929 | 3.168 |

| | MEETING THE TARGET | | |
|---|---|---|---|
| | Mean Error | s.d | RMS Error |
| S1 | 1.329 | 9.367 | 9.146 |
| S2 | 2.917 | 3.470 | 4.398 |
| S3 | -0.300 | 0.690 | 0.727 |
| S4 | 1.758 | 2.683 | 3.113 |
| S5 | 2.640 | 3.694 | 4.423 |
| S6 | -0.089 | 3.790 | 3.642 |
| MEAN | 1.376 | 3.949 | 4.242 |

(b) Percentage of Movement Time

| | Known Static | Unknown Static | Chasing | Meeting |
|---|---|---|---|---|
| S1 | 89.031 | 15.119 | 14.083 | 18.729 |
| S2 | 90.282 | 15.221 | 15.705 | 18.652 |
| S3 | 91.855 | 14.960 | 17.374 | 14.786 |
| S4 | 91.977 | 12.559 | 12.153 | 14.944 |
| S5 | 87.194 | 17.767 | 12.358 | 14.857 |
| S6 | 91.669 | 14.444 | 15.026 | 13.617 |
| | | | | |
| Mean | 90.335 | 15.012 | 14.450 | 15.931 |
| s.d. | 1.916 | 1.673 | 2.012 | 2.192 |

(c) Duration of t-coupling

| | Known Static | Unknown Static | Chasing | Meeting |
|---|---|---|---|---|
| S1 | 323.069 | 41.500 | 39.947 | 57.460 |
| S2 | 286.338 | 47.700 | 49.438 | 63.440 |
| S3 | 285.317 | 47.494 | 60.220 | 47.462 |
| S4 | 281.900 | 41.669 | 40.323 | 51.883 |
| S5 | 328.325 | 46.922 | 44.918 | 52.885 |
| S6 | 402.300 | 49.233 | 49.670 | 48.208 |
| | | | | |
| Mean | 317.875 | 45.753 | 47.419 | 53.556 |
| s.d. | 46.071 | 3.319 | 7.556 | 6.032 |

(d) Gaze-target angle 100ms prior to coupling onset

| | Known Static | Unknown Static | Chasing | Meeting |
|---|---|---|---|---|
| S1 | 133.968 | 65.012 | 57.267 | 70.767 |
| S2 | 125.186 | 67.159 | 60.749 | 65.233 |
| S3 | 126.107 | 60.923 | 59.746 | 60.981 |
| S4 | 120.077 | 56.844 | 50.537 | 53.977 |
| S5 | 127.247 | 42.288 | 30.381 | 44.874 |
| S6 | 149.499 | 59.160 | 60.467 | 56.061 |
| | | | | |
| Mean | 130.347 | 58.564 | 53.191 | 58.649 |
| s.d. | 10.388 | 8.823 | 11.807 | 9.098 |

(e) Gaze-target velocity 100ms prior to coupling onset

| | Known Static | Unknown Static | Chasing | Meeting |
|---|---|---|---|---|
| S1 | 49.913 | 627.876 | 548.368 | 579.879 |
| S2 | 21.189 | 508.729 | 496.287 | 500.256 |
| S3 | 17.626 | 547.919 | 536.310 | 545.612 |
| S4 | 33.851 | 450.228 | 422.257 | 459.393 |
| S5 | 59.104 | 458.016 | 418.338 | 509.861 |
| S6 | 12.988 | 474.730 | 457.683 | 491.508 |
| | | | | |
| Mean | 32.445 | 511.250 | 479.874 | 514.418 |
| s.d. | 18.669 | 67.593 | 56.115 | 42.502 |